University of Alberta

Patterns in Habitat Quality for the White-throated Sparrow (*Zonotrichia albicollis*) in a Recently Logged Landscape.

by

Kevin C. Hannah ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Master of Science

in

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ABSTRACT

Although White-throated Sparrows (*Zonotrichia albicollis*) are not thought to be negatively impacted by forest harvesting, significant range-wide declines have been documented in recent decades. I conducted a detailed, population-level study of this species in a recently harvested landscape near Calling Lake, Alberta. My results suggest territory density provides a poor measure of habitat quality for this species. Comparisons between forest/clearcut edges, 5-6 year old clearcuts, and interior forests, using various reproductive indices, suggest habitat quality was highest in interior forests, and lowest in recent clearcuts. Breeding chronology, site fidelity, and dispersal were not good measures of habitat quality. My results emphasise the need to collect habitat quality data, beyond simple measures of density. Short-term studies not measuring habitat quality should be carefully evaluated prior to deciding on management actions.

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CHAPTER 1 – THESIS INTRODUCTION

1.1 – Scope and rationale for the study

Birds represent one of the best known and well studied taxonomic groups in the world (Newton 1998). With over 9600 species occurring globally (Sibley and Monroe 1990), birds occupy and utilise almost every terrestrial ecosystem on earth (Gill 1995). However, given their high degree of habitat specialisation, birds can be susceptible to habitat alteration and contamination (Elliot et al. 1994, Bishop et al. 1995, Gochfeld and Burger 1998). In recent years, birds have increasingly become indicators of declining ecological integrity (Parr 1994). Nearly twenty percent of all bird species face some risk of extinction, and most of the remaining eighty percent are in decline (Tucker and Heath 1994). Declining bird populations signal the importance of increasing efforts to protect and better manage remaining habitats, and to restore habitats where ecological integrity is no longer intact.

As with most forested areas of the world, the mixed-wood boreal forest of northern Alberta has seen an enormous increase in recent industrial development, prompting concern for bird populations in the region. Within the last decade, the majority of the province's forested lands have been leased to forestry companies, with little or no prior knowledge of much of the region's avifauna (Schmiegelow and Hannon 1993). This paucity of data has spawned an enormous interest in forest harvest and fragmentation studies throughout the boreal region of Alberta (Westworth and Telfer 1993, Scheick et al. 1995, Norton and Hannon 1997, Schmiegelow et al. 1997, Song 1998, Tittler 1998). Knowledge generated from these studies, if incorporated into forest

harvesting plans, may allow for more adaptive approaches to wildlife management (Walters 1986, Kessler et al. 1992). Despite a marked increase in fragmentation studies on birds in the western boreal forest in recent years, most have been community-level studies measuring changes in relative abundance or density. Although this form of assessing response is more financially and logistically feasible than detailed, population-level studies, it may provide less accurate information for the management or conservation of the region's avifauna.

Nearly two decades have passed since the seminal paper by Van Horne (1983), warning of the dangers of using only density or relative abundance as metrics of habitat quality in studies of wildlife-habitat associations. Even in the recent literature, relationships between density and reproductive success in birds are tenuous (Vickery et al. 1992b, Purcell and Verner 1998, Rangen et al. 2000). Despite both the early warnings by Van Horne (1983), and those in the recent literature, few published studies in the western boreal region have attempted to measure indices such as reproductive success or survival. Although both parameters are costly to measure, they may provide more sensitive measurements of actual responses of forest birds to habitat alteration than density or relative abundance.

1.2 – Natural history of the study species

The White-throated Sparrow (*Zonotrichia albicollis*) is one of the best studied songbirds in North America (Falls and Kopachena 1994). It is a large, conspicuous, and very common passerine, breeding throughout most of Canada's forested regions (Falls and Kopachena 1994). It builds a cup-shaped nest on or near the ground, which is usually concealed by ground vegetation (Lowther and Falls 1968, Falls and Kopachena

1994). The White-throated Sparrow is highly opportunistic with respect to food selection; insects, supplemented with greens and fruit are the preferred diet in summer (Falls and Kopachena 1994). The species has been described most often as a habitat generalist (Darveau et al. 1995, Germaine et al. 1997, Norton and Hannon 1997), occasionally as an early successional species (Canterbury and Blockstein 1997), or as an edge dependent species (Clark et al. 1983).

Several recent studies conducted in the nearctic boreal forest have monitored short-term community responses of songbirds to different forest harvest prescriptions (Westworth and Telfer 1993, Darveau et al. 1995, Scheick et al. 1995, Norton and Hannon 1997, Rail et al. 1997, Schmiegelow et al. 1997, Song 1998, Tittler 1998). Results of these studies suggest some geographic differences in responses of White-throated Sparrows to habitat alteration. Studies conducted in the east have consistently found slight, short-term population increases in response to forest harvest (Canterbury and Blockstein 1997, Germaine et al. 1997, Darveau et al. 1995). In studies conducted in the west, population responses are generally neutral, or slightly positive (Westworth and Telfer 1993, Norton and Hannon 1997, Song 1998, Tittler 1998). Only one study indicated a slight decrease in overall White-throated Sparrow relative abundance following forest harvest (Schmiegelow et al. 1997).

Results from Canada-wide Breeding Bird Survey (BBS) data suggest that significant annual population declines (-1.1%) have occurred between 1966 and 1996 (Downes et al. 1999). Despite the apparent lack of sensitivity of this species to forest harvest, some mechanism is responsible for its overall decline. It is possible that due to sampling methodology (i.e. community level point counts) which measure relative

abundance, and the short duration of most studies (2-3 years) after forest harvesting, actual, long-term responses of this species are not being detected, nor accurately measured. By measuring population responses directly, I wanted to determine if results were similar to community studies, and identify potential mechanism(s) for any differences.

1.3 – Statement of purpose

The major objective of this thesis was to assess White-throated Sparrow population responses to forest harvesting. I also address a range of issues surrounding the use of density as an indicator of habitat quality. In Chapter 2, I compared White-throated Sparrow territory density to a number of different habitat quality indices, including various measures of reproductive success. My goal was to assess how accurately density reflected actual habitat quality. In Chapter 3, I compared habitat quality for White-throated Sparrows between clearcut, edge, and interior forest habitats in a recently harvested, forested landscape. In Chapter 4, I use breeding chronology, site fidelity, and dispersal as three additional parameters to measure habitat quality for this species across the same three habitat treatments. In my final chapter, I present a synthesis of my results, and their relevance to managing White-throated Sparrow and other songbird populations in the western boreal forest. To conclude, I provide some directions for future research and identify some fundamental problems with current census methods.

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CHAPTER 2 – HABITAT QUALITY FOR THE WHITE-THROATED SPARROW: IS DENSITY A MISLEADING INDICATOR?

2.1 – Introduction

Traditionally, the density of a species in a particular habitat was thought to reflect available resources (Fretwell and Lucas 1970, Lancia et al. 1982, Maurer 1986). Correspondingly, it was assumed that in habitats where individuals of a species occurred at high density also exhibited higher individual reproductive output or increased survival over those with lower density (see Newton 1998). Van Horne (1983) challenged this assumption, suggesting that the relationship between density and habitat quality may be de-coupled, due to temporal habitat variability or intra-specific dominance interactions within different habitats. More specifically, she suggested that older individuals in high quality habitat may produce a surplus of young in good years, which would emigrate into nearby low quality habitat. High densities of young, inexperienced birds in low quality habitat may suffer low reproductive output and high mortality, thereby de-coupling the relationship between density and habitat quality (Fretwell and Lucas 1970), and creating asymmetric gene flow between habitats (Dias 1996). Van Horne (1983) recommended that assessments of habitat quality include components of density, reproductive success, and survival.

In some recent studies, density has been compared with reproductive success as a means of assessing habitat quality (Vickery et al. 1992b, Purcell and Verner 1998, Rangen et al. 2000), however estimating reproductive success can be time consuming (Vickery et al. 1992a). In addition to commonly [illegible]asures such as reproductive

success and territory density, other indices may also provide clues to the quality of different habitats. Such indices include aspects of food quality or availability, pairing success, and behavioural time-budgets. Body condition of breeding birds may be a strong correlate of the quality or availability of food and thus be a good indicator of habitat quality. Poor body condition may limit reproduction and reduce survival in birds (Martin 1987, Arcese and Smith 1988, O'Halloran et al. 1990, Selman and Houston 1996, Haas 1998). In addition, the pairing success of male birds in different habitats may also be a strong correlate of habitat quality (Wander 1985, Gibbs and Faaborg 1990, Villard et al. 1993, Hunt 1996), as females may avoid territorial males in poor quality habitat.

The time birds allocate to a specific behaviour may also provide some indication of habitat quality (O'Halloran et al. 1990). Male singing may function to attract a female (Møller 1991, Falls and Kopachena 1994), signal to other males an established territory (Rodrigues 1996), or a paired high quality territorial male (Møller 1991). For males which are paired, singing may function as a 'keep out' signal (Hanski and Lamila 1993, Sheldon 1994, Slagsvold et al. 1994), indicating an individual's paired status or fitness to competing males (McShea and Rappole 1997). Differential investment in singing may largely be in response to density-dependent competition (Bryant and Tattner 1988, O'Halloran et al. 1990). If density is a good indicator of habitat quality, then investment in singing may increase in response to increasing density, and increasing habitat quality. Alternatively, pairing status can affect song rate, whereby unpaired males may sing more frequently than paired males (Gibbs and Faaborg 1990, Gibbs and Wenny 1993, Porneluzi et al. 1993). Paired males may have to allocate more time to singing in plots with low overall pairing success as a means of protecting their mates. Therefore, in poor

quality habitats, where pairing success may be lower, investment in singing may be higher. In either case, investment in singing may be costly, especially if it compromises the amount of time that an individual spends foraging (Ydenberg and Krebs 1987, Askenmo et al. 1992).

The proportion of time an individual bird allocates to foraging, however, may not be reflected in the body condition of that bird. Differences in the efficiency with which an individual bird forages may better reflect patterns in body condition than overall foraging time. Knapton and Falls (1983) suggest that White-throated Sparrows preferentially prey on lepidopteran larvae, a potentially rare food resource compared to other, more available foods (seeds, greens etc.). After male White-throated Sparrows were experimentally removed from breeding territories, single females compensated for reduced male provisioning by selecting larger, and potentially rarer, insect prey items, than control females (Whillans and Falls 1990). In periods of time constraint, such as those imposed by increased territorial defence, individuals may maximise foraging efficiency by selecting rarer, high quality food items. In order to exploit these rarer prey items, experienced foragers may travel greater distances during foraging bouts than inexperienced foragers (Zach 1979).

The White-throated Sparrow is one of the most widely distributed and abundant breeding songbird species throughout Canada's forested regions (Falls and Kopachena 1994). Occurring south of the tree line and predominantly east of the Rocky Mountains, this species exhibits enormous habitat plasticity (Falls and Kopachena 1994). It has been described most often as a habitat generalist (Westworth and Telfer 1993, Scheick et al. 1995, Darveau et al. 1995, Germaine et al. 1997, Rail et al. 1997, Schmiegelow et al.

1997, Song 1998), occasionally as an early successional species (Canterbury and Blockstein 1997), or as an edge dependent species (Clark et al. 1983). Although known to breed commonly within forest, White-throated Sparrows have also been documented establishing territories and nesting in recent clearcuts (Darveau et al.1997, Schmiegelow et al. 1997, Tittler et al. 2000). Given the apparent generalist nature of this species, and its high relative abundance, it is an ideal candidate in which to investigate the relationship between density and habitat quality across a range of different habitats.

I studied White-throated Sparrow density in relation to habitat quality in a fragmented and highly variable habitat matrix to determine if density was accurately reflecting indices of habitat quality. Habitat quality was assessed through the use of five parameters, including: reproductive success (measured using a reproductive index), pairing success, body condition (both proportional body condition and interclavicular fat score), and proportion of time allocated to foraging. To evaluate these relationships, I tested the following predictions:

If density is a good predictor of habitat quality, then:

1) reproductive success should increase with increasing species density,

2) body condition of birds should increase with increasing density,

3) the proportion of time spent singing should increase with increasing density, resulting in less time spent foraging, however foraging efficiency should be greater

Additionally, since reproductive success has been a standard index in assessments of habitat quality, I wanted to compare how well the other habitat quality indices I used were correlated with reproductive success. My goal with this comparison was to evaluate

if other indices could potentially act as surrogates for reproductive success in assessments of habitat quality.

2.2 - Methods

2.2.1 - *Study Area*

This study was conducted in mixed-wood boreal forest near Calling Lake, Alberta (55°15'N, 113°19'W), in 1998 and 1999, as part of the Calling Lake Fragmentation Studies (see Schmiegelow et al. 1997). My study design consisted of three, ten hectare (250 X 400 m) plots located in three different habitat types (interior forest, edge, and recent clearcuts), each replicated three times (Figure 2.1). Interior forest treatments consisted of mixed stands of old (120-140 yr.) trembling aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*), white spruce (*Picea glauca*), and white birch (*Betula papyrifera*). Interior forest plots were located a minimum of 200 m from a forest/clearcut edge. Edge treatments also consisted of old, mixed forest stands and extended from the forest/clearcut interface to 125 m into the forest. Clearcut plots were in 5-6 year old secondary forest, 250 m wide, and were surrounded by older, mixed forest (edge plots). The clearcuts did not receive any site treatment following harvest, and contained 1-2.5 m regenerating aspen and poplar. Sets of clearcut and edge plots were located immediately adjacent to each other; replicates and interior forest plots were a minimum of 150 m apart.

2.2.2 - *Bird Territory Density*

I used spot-mapping to determine White-throated Sparrow density (Robbins 1970). Spot-mapping consisted of twelve census 'rounds' conducted from 16 May to 23

July in 1998, and sixteen census 'rounds' from 2 May to 25 July in 1999. Plots were spatially referenced using a 50 X 50 m grid, permitting ready identification of points on survey sheets. To reduce potential sampling biases, I alternated observers and start locations for each plot on each census round. I began each census at dawn and continued for a maximum of six hours, to ensure sampling was conducted during the peak hours of male territorial singing. A census was halted in high winds or heavy precipitation. A territory was considered occupied if a bird was detected singing in the same area for a period of at least ten days, was paired, or showed any evidence of nesting (Robbins 1970). In calculating density, only those territories with greater than fifty percent of mapped locations occurring within the plot were included in the analysis. Territories that bordered the forest/clearcut interface were allocated to either habitat if greater than fifty percent of the detections occurred in that habitat.

2.2.3 - *Body Condition*

I captured White-throated Sparrows in mist nets using song playbacks. Each captured bird was given a unique combination of 2 (1998), or 3 (1999) coloured plastic leg bands and one U. S. Fish and Wildlife Service aluminium band. For each captured bird, I determined sex through a combination of wing length and presence of brood patch or cloacal protuberance (Pyle et al. 1997). However, I was unable to confidently determine the age of second year birds using Pyle et als. (1997) description. Several recaptured birds known to be at least in their third year had plumage indicative of birds in their second year, using their criteria (unpubl. data). I measured wing length to the nearest millimetre using unflattened wing chord, and body mass to the nearest gram using a 50 g Pesola spring balance. I estimated the body condition of birds by using the ratio of

body mass (g) to wing chord length (mm) (Winker et al. 1992) and interclavicular fat scores (Haas 1998). Fat was scored on a scale from 0 (no visible fat) to 2 (fat filling the cavity) at intervals of 0.5. Since birds captured throughout the season were used in determining body condition in each plot, I tried to vary the time of capture of birds in plots both daily and seasonally to average out temporal variation in body condition.

2.2.4 - *Reproductive Success*

I measured reproductive success using a reproductive index (Vickery et al. 1992a) and by observing actual nests. Using the index method, territories were ranked on a scale from 1 to 5 on the basis of behavioural cues with increasing evidence of reproductive success (Table 2.1). I assessed two parameters: proportion of territories per plot in which a male bird was paired, and the proportion of territories per plot which produced ≥ 1 fledgling. Although these methods were not independent measures, I was interested in determining if reduced pairing success led to reduced reproductive success.

Calculations of territory density are based on the presence of a territorial male for a minimum of 10 days (Robbins 1970), whereas the reproductive index method of Vickery et al. (1992a) requires a territorial male to be present for a minimum of 4 weeks. These differences between methods resulted in fewer territories for analysis using the reproductive index method than for calculations of territory density, due to the increased residency requirement.

2.2.5 - *Time Budgets*

I followed colour banded males to determine if there were differences in the amount of time invested in singing or foraging in plots of differing density. Time budget data were collected between 5 June and 19 July in 1999. Because time allocated to

different behaviours can be significantly different between paired and unpaired males (Gibbs and Faaborg 1990, Porneluzi et al. 1993, McShea and Rappole 1997), I only followed males that were paired with a female. I avoided collecting data during the nestling and fledgling periods as determined from monitored nests, because the demands of feeding young may alter an individual's behavioural-time budget. If a male sparrow was observed carrying food or was observed with a fledgling sparrow, I terminated the sampling bout and these data were not used in the analysis. Sampling bouts, where I followed an individual male for less than 5 minutes, were also excluded. If I lost contact with a bird, I spent a maximum of 15 minutes attempting to re-sight the individual before terminating the sampling bout. I only recorded data when I could detect a bird visually, or audibly while the bird foraged on the ground. I recorded behaviour at 15 second intervals while I mapped the movement of individual birds on the alphanumeric grids within each plot. For each individual bird, I spent a maximum of 30 minutes on each bout, and each individual was observed on a maximum of four bouts.

My behaviour classifications were based on those of Askenmo et al. (1992). Six types of behaviour were thought to represent all distinguishable activities in the field. However, for the purposes of this study, I include only singing and foraging behaviour.

1) Singing occurred mainly from a few song posts, typically elevated from surrounding vegetation. At times singing bouts occurred at the tops of trees, but could occur at any height above the ground. Singing incorporated both the actual delivery of song and the 10-15 second intersong interval (Falls and Kopachena 1994).

2) Foraging included any activity thought to represent searching for, catching, or consuming prey. The majority of White-throated Sparrow foraging takes place on the

ground where insects are uncovered through a technique involving 1- 4 rapid kicking motions where the leaf litter is cleared away (Falls and Kopachena 1994). This type of foraging is quite conspicuous and birds can be easily tracked when engaging in this activity. Birds also glean insects in small, low shrubs and will infrequently pursue aerial insects through 'hawking'.

2.2.6 - *Foraging Efficiency*

In addition to the temporal data I collected on individual bird time-budget behaviour, I also recorded the distances birds travelled while foraging, using the spatially-referenced grid within each plot. After each individual observation bout, mapped foraging routes were summarised into a linear distance measure for each bout. Foraging efficiency was measured by the ratio of distance travelled (m), to the time spent foraging (minutes). All foraging efficiency data were summed for each individual to calculate an overall mean ratio of foraging efficiency per individual. Based on the assumption that more experienced, higher quality individuals exploited rarer, more patchily distributed, but higher quality, food resources, a higher ratio was interpreted to indicate greater efficiency.

2.2.7 - *Statistical Analyses*

All proportional data were arcsine $\sqrt{p}$ transformed prior to analysis, where p represents a proportion (Zar 1996). A Kolmogorov-Smirnov goodness of fit test with Lillefors correction was used to examine the normality of both my dependent and independent variables. I tested for homogeneity of variances using Levene's test (SPSS 1999). I tested for differences between years in my habitat quality indices (independent variables) using paired sample t – tests. All habitat quality data was averaged over both

years, and an overall mean was used for analysis. To test for relationships between density and indices of habitat quality, I used linear regression. Prior to analysis, I constructed a bivariate correlation matrix for each year separately using Pearson correlation coefficients to reduce chances of multicollinearity between independent variables (Zar 1996).

To evaluate the relationship between singing, foraging, foraging efficiency and body condition, I used linear regression. For examination of the relationship between reproductive success (dependent variable) and indices of habitat quality (independent variables), I used stepwise multiple regression. Again, I constructed bivariate correlation matrices for all independent variables using Pearson correlation coefficients. Correlated independent variables ($p \leq 0.05$) were tested against the dependent variable (reproductive success), in a separate model. I used a probability of 0.05 for entry and a probability of 0.10 for removal in all models.

In all analyses, I considered an alpha ≤ 0.05 to be highly significant and an alpha ≤ 0.10 to be marginally significant. All data are presented as mean $\pm$ SE. All analyses were performed using SPSS (Version 10.0) (SPSS 1999).

2.3 – Results

2.3.1 – *Territory Density*

A total of 123 White-throated Sparrow territories were established over all plots in 1998; 107 territories were established in 1999. Territory density ranged from 7 to 17 territories per 10 ha plot (mean 13.67 $\pm$ 1.13) in 1998, and from 7 to 21 territories per 10

ha plot (mean 11.89 ± 1.52) in 1999 (Figure 2.2). Between years, territory density was variable, but differences were not significant ($t = 0.938$, $p = 0.36$).

2.3.2 – *Habitat Quality Variables*

A total of 130 White-throated Sparrows were captured and banded over all plots and years (Table 2.2). Of these, 93 (71.5%) were male and 37 (28.5%) were female. Both proportional body condition and interclavicular fat score were calculated using different birds captured at different times during the season in each plot. Repeated recapture of individuals was not possible, as bird responses to song playback decreased dramatically following initial capture. Some females were captured only during the nesting period and may have been investing in the production of eggs, rather than storing fat, thereby biasing results. Sample sizes for females on a plot by plot basis were also very low, so female body condition data were not used in analyses. Males provided a better representation, with greater sample sizes and less temporal variation in body mass during the breeding season than females (unpubl. data).

I estimated reproductive ranks for 105 territories in 1998 (mean, 11.7 ± 1.13 territories per plot) and 98 territories in 1999 (mean, 10.9 ± 1.43 territories per plot). Reproductive success, measured by the percentage of territories in each plot which successfully produced at least one juvenile (a rank of 5), was highly variable both between plots and between years. In 1998, reproductive success averaged 37.4 ± 6.88 % per plot (range 8-67%), and in 1999, reproductive success averaged 28.4 ± 4.93% per plot (range 0-50%), however differences were not significant (Figure 2.3). I was unable to compare density and reproductive success using actual nests, as my sample size (n = 31), was insufficient for analysis. Male pairing success was also highly variable both between

plots and between years. In 1998, pairing success averaged 53.8 ± 8.58 %, and in 1999, pairing success averaged 66.4 ± 4.82 %, however differences between years were not significant.

For all habitat quality indices, except proportional body condition, differences were not significant between years (Table 2.3). Although significant differences existed in proportional body condition between years, I pooled data from both years because, although mean body condition was greater in 1998 than 1999, I was less interested in the inter-annual variation than in the overall pattern between plots. When compared to density for each year individually, body condition was not significantly related (density - 1998: $R^2 = -0.09$, $p = 0.58$; 1999: $R^2 = -0.14$, $p = 0.99$).

2.3.3 – *Density as an Indicator of Habitat Quality*

Overall, density was a poor predictor of habitat quality (model $R^2 = -0.56$, $df = 4$, $p = 0.88$) (Table 2.3). Contrary to my prediction, rates of singing were not significantly related to territory density. Given this result, the allocation of time to singing behaviour does not seem to increase in a density-dependent manner. My alternate hypothesis, that overall rates of pairing success in each plot may strongly influence the proportion of time an individual allocates to singing was also incorrect. The proportion of time allocated to singing was not significantly related to proportional pairing success ($R^2 = -0.13$, $df = 1$, $p = 0.75$).

2.3.4 – *Relationships among indices of habitat quality*

If high investment in singing results in less time foraging, the result may be reduced body condition, and ultimately, reduced reproductive success. The proportion of time birds allocated to singing was highly correlated with the proportion of time allocated

to foraging ($R^2 = 0.85$, $df = 1$, $p \leq 0.001$). However, foraging was not significantly related to male proportional body condition ($R^2 = -0.14$, $df = 1$, $p = 0.97$), or male fat score ($R^2 = -0.13$, $df = 1$, $p = 0.77$). Foraging efficiency was also not significantly related to male proportional body condition ($R^2 = 0.07$, $df = 1$, $p = 0.26$), or male fat score ($R^2 = 0.25$, $df = 1$, $p = 0.12$)

2.3.5 – *Evaluation of Habitat Quality Indices*

Of the indices I used to assess habitat quality, only male proportional body condition and proportional pairing success were significant predictors of reproductive success (rank 5) (model; $R^2 = 0.85$, $df = 2$, $p \leq 0.001$). Male fat score and proportion of time allocated to foraging were not related to reproductive success.

2.4 – Discussion

2.4.1 – *Is density an indicator of habitat quality?*

My results indicate that density of White-throated Sparrows in a recently harvested and patchy landscape was not related to habitat quality. Numerous other studies have also shown that density and breeding success are not correlated in many passerine bird species (Maurer 1986, Vickery et al. 1992b, Purcell and Verner 1998, Rangen et al. 2000). Few, however, have compared density with other indices of habitat quality. I used reproductive success and three additional indices of habitat quality, and conclude that the link between habitat quality and density for the White-throated Sparrow in my study area is de-coupled.

As Van Horne (1983) contended, large numbers of immature birds may occupy poor quality habitat in high densities, thereby de-coupling the relationship between

density and habitat quality. It is possible that White-throated Sparrows, settling different quality habitats at different densities, were doing so by age or dominance. Those plots in which a high proportion of birds obtained mates or successfully reproduced may also have had a high proportion of older birds. Other studies have observed higher proportions of adult birds in habitats with higher relative reproductive success or pairing success, with less successful, immature birds occupying marginal habitat or becoming non-territorial 'floaters' (Bollinger and Gavin 1989, Sherry and Holmes 1989, Hunt 1996). However, I could not distinguish second year birds from those which were older than second year. Further study of the morphology of White-throated Sparrows of known age and sex would be beneficial in this regard.

As predicted, the proportion of time an individual male allocated to singing was highly correlated with the proportion of time an individual allocated to foraging. In habitats where individuals allocate large amounts of time to territorial singing, reduced foraging time may result in poorer body condition. However, proportion of time allocated to foraging was not significantly related to male body condition, as reflected by both proportional body condition and male fat score. If high quality individuals are also more experienced and efficient foragers, then a relationship between proportional time spent foraging and body condition may not exist. No significant relationship existed between foraging efficiency, as defined by the ratio of foraging distance to foraging time, and the body condition of male birds. Sample sizes for foraging efficiency were quite low, and variability between individuals was high, thereby my ability to detect differences in foraging efficiency may have been low. Alternatively, individuals which travel greater distances in search of food may not be efficient foragers, especially if the

benefits of capturing larger, rarer prey items does not exceed the energetic costs of added travel (Trandem and Lampe 1993). Data on White-throated Sparrow prey selection and foraging behaviour would be beneficial in order to better quantify foraging efficiency.

Proportional allocation of time to singing did not increase in a density-dependent manner, as density and proportion of time allocated to singing were not related. All males used in behavioural comparisons were paired, suggesting that individuals between plots should allocate time to singing for similar reasons, although potentially in different proportions. However, if the sub-sample of birds used in behavioural time-budgets represents both dominant and subordinate birds with unequal competitive abilities, then density-dependent patterns in the allocation of time to different behaviours may not emerge.

My alternate hypothesis, that paired males would allocate more time to singing in plots with low relative rates of pairing success was also not supported. The allocation of time to singing in male White-throated Sparrows was not related to the proportion of paired individuals in a plot. Paired males in plots with low overall pairing success did not allocate a larger proportion of time to singing than did paired males in plots with higher relative rates of pairing success. Several authors have shown that the function of territorial song may differ between passerine bird species (Hanski and Lamila 1993, Sheldon 1994, Martin-Vivaldi et al. 1999). The function of post-dawn singing in the White-throated Sparrow may not be to advertise the status of a paired male, as in some species (Slagsvold 1996, Pinxten and Eens 1998). Further insight into the role of post-dawn territorial singing in White-throated Sparrows would is needed.

The body condition of birds was also not related to density. Neither proportional body condition nor fat score of individual males revealed discernible patterns related to territory density. If food abundance or availability is high in all plots, birds may allocate more time to other behaviours instead of continuing to invest in feeding and accumulating fat (Wiens 1983). Generally, food is not thought to be limited for birds during the breeding season, largely because food is abundant during this period, populations are generally below carrying capacity, and population responses to changing environmental conditions, namely food levels, is slow (Wiens 1977, 1983, Hutto 1985, Martin 1986).

2.4.2 – *Evaluation of habitat quality indices*

Of the indices that I used to measure habitat quality, both male pairing success and proportional body condition were significant predictors of reproductive success (rank 5). Male pairing success has been used to measure habitat quality in numerous other studies (Gibbs and Faaborg 1990, Villard et al. 1993, Holmes et al. 1996, Hunt 1996). Pairing success should be a strong correlate of reproductive success, largely because reproductive success should be higher in plots where more males are paired (Hunt 1996).

Proportional body condition was also correlated with reproductive success (rank 5), suggesting that the body condition of male White-throated Sparrows may be a precursor to reproductive success (see Martin 1987). Plots in which males were in poor body condition experienced lower overall reproductive success than did males in plots with higher overall body condition. Differences in male body condition between plots did not appear to be a result of differences in either rates of male foraging, or in male foraging efficiency. This suggests that both the availability of food and the efficiency

with which individuals could acquire food were not responsible for differences in male body condition. Possibly, differences in male body condition may reflect the quality of either wintering sites or migratory stopover sites, and not the quality of sites on the breeding grounds. Individuals starting the breeding season in better condition may be more likely to experience natural nesting success than those in poor relative body condition (Haas 1998).

2.4.3 – *Conservation and management implications*

Reproductive success, a commonly used index of habitat quality, was not significantly correlated with density, suggesting that density alone is misleading. In fact, of the five indices of habitat quality that I measured, none were correlated with White-throated Sparrow territory density. Studies which have relied on density alone may be accurately measuring how a species is distributed across a range of habitats, but may be drawing incorrect conclusions with respect habitat quality. Therefore, in a conservation context, management decisions based on studies using only density as an indicator of habitat quality may exacerbate and not abate potential declines of some songbird species. In future studies, density should be compared with reproductive success or another index of productivity to better assess habitat quality. Only then can appropriate management options be invoked to maintain or enhance habitat quality for a particular species. Given the strong relationship between reproductive success and both male pairing success and male body condition, continued use of these indices as a means of evaluating reproductive success seems warranted.

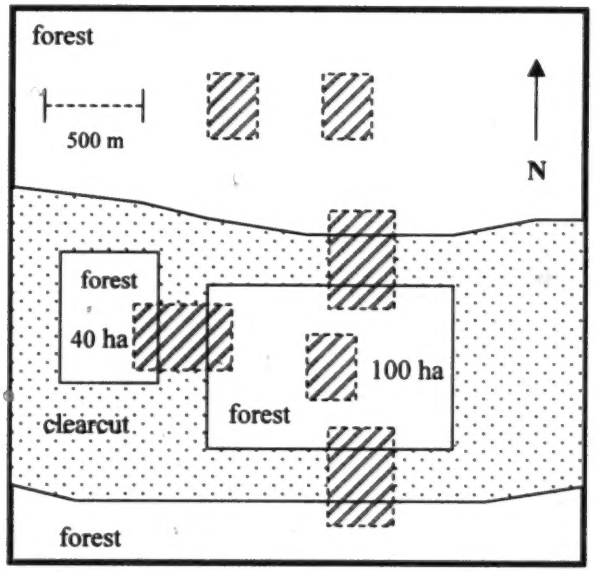

Figure 2.1 – Diagram of study area showing forested and non-forested (dotted) areas, location of study plots (hatched boxes), and sizes of forest blocks.

Rank	Definition
1	Territorial male present 4+ weeks.
2	Territorial male and female present 4+ weeks.
3	Pair found nest building, laying or incubating eggs or giving Distraction display.
4	Adults carrying food to presumed nestlings.
5	Evidence of fledgling success.

Table 2.1 – Reproductive index rankings and definitions (after Vickery et al. 1992a).

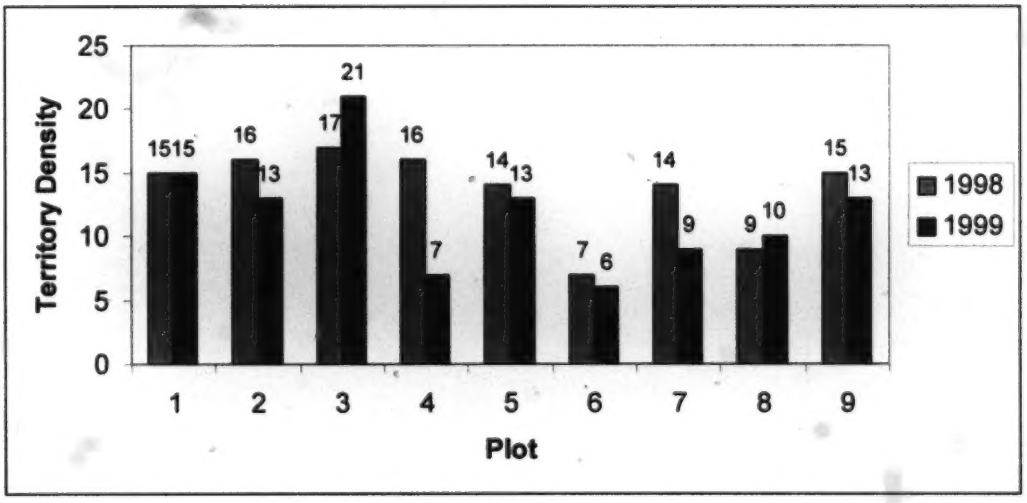

Figure 2.2 – Territory density of White-throated Sparrows by plot in both 1998 and 1999. Plots are located in edge habitat (1-3), clearcuts (4-6), and interior forest (7-9).

		Plot									
Year	Sex	1	2	3	4	5	6	7	8	9	Total
1998	Male	7	9	10	1	4	1	6	6	8	52
	Female	5	4	6	0	1	1	1	0	4	22
1999	Male	2	8	9	5	2	3	1	6	5	41
	Female	1	2	4	1	0	1	2	2	2	15
									Grand Total		130

Table 2.2 – Summary of captured White-throated Sparrows for each plot by year and sex. Plots are located in edge habitat (1-3), clearcuts (4-6), and interior forest (7-9).

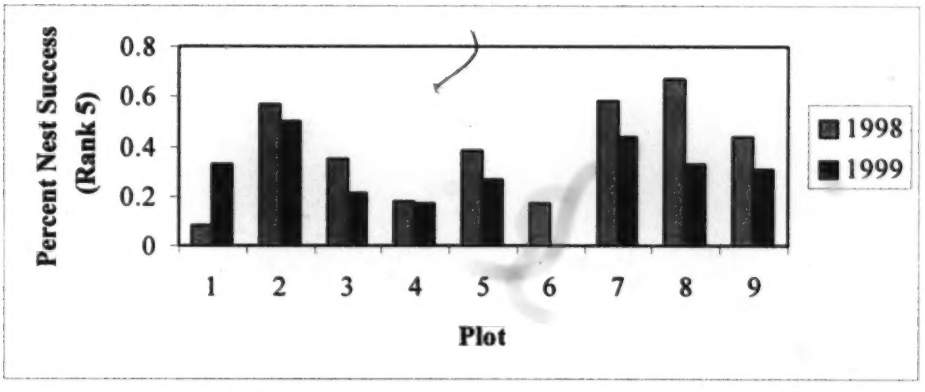

Figure 2.3 – Mean proportional reproductive success (rank 5) per plot as determined through use of reproductive index method (Vickery et al. 1992a), for 1998 and 1999. Plots are located in edge habitat (1-3), clearcuts (4-6), and interior forest (7-9).

Variable	*t*	*df*	*p* - value
Mean Breeding Rank	1.36	16	0.19
Reproductive Success	0.07	16	0.95
Pairing Success	-1.29	16	0.22
Body Condition	2.52	16	0.02*
Fat Score	-0.53	16	0.6

Table 2.3 – Summary of paired sample *t* – test results for habitat quality indices between 1998 and 1999. Mean breeding rank represents overall plot means using reproductive index method (Vickery et al. 1992a). Reproductive success represents proportion of territories per plot with rank of 5 (≥ 1 fledgling). Body condition represents overall mean proportional body condition (g/mm) per plot.

Model	Variable	R^2	*df*	F or *t*	*p* - value
1	Model	-0.46	4	0.38	0.82
	Rank 5			0.15	0.87
	Body Condition			0.37	0.73
	Fat score			-0.93	0.41
	Foraging			0.63	0.57
2	Model	0.01	1	1.05	0.34
	Rank 5			1.03	0.34

Table 2.4 – Summary of linear regression models comparing territory density with habitat quality indices. Results for overall models and for individual components in each of the models are presented. F – statistics are ANOVA results of overall models and *t* – statistics are for individual variables.

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CHAPTER 3 – HABITAT QUALITY FOR THE WHITE-THROATED SPARROW: IMPLICATIONS OF FOREST HARVESTING.

3.1 – Introduction

In recent decades, declines in many migratory passerine songbirds have been linked to increased habitat fragmentation (Hagan and Johnston 1992), leading to reductions in the amount of high quality habitat for certain species. Although highly debated, the most likely causal explanation for these declines has been loss of forest habitat throughout the breeding ranges of these species (Sherry and Holmes 1993, Böhning-Gaese et al. 1993, Robinson and Wilcove 1994, but see Sherry and Holmes 1996). Harvesting of forest habitat can result in an increased amount of edge (Whitcomb et al. 1981, Yahner 1988), reductions in the amount of 'interior' forest (Rich et al. 1994), changes in vegetation structure (Ranney et al. 1981, Fraver 1994), and degradation and isolation of remaining habitat (Robinson et al. 1995). Birds breeding at or near edges may be susceptible to increased rates of nest predation or parasitism (Gates and Gysel 1978, Brittingham and Temple 1983, Gates and Giffen 1991), or increased competition (Ambuel and Temple 1983, Scheick et al. 1995, Hagan et al. 1996), thereby exacerbating habitat loss and further reducing habitat quality.

In most habitat fragmentation studies conducted in the nearctic boreal forest, responses of forest songbirds to forest harvesting has been measured by changes in density or relative abundance (Westworth and Telfer 1993, Darveau et al. 1995, Schieck et al. 1995, Darveau et al. 1997, Schmiegelow et al. 1997, Song 1998). Relying on density alone in assessments of population responses to habitat alteration or loss can be misleading (Van Horne 1983, Vickery et al. 1992b, Purcell and Verner 1996, Rangen et

al. 2000, Chapter 2). Also of concern is the limited temporal scale of some studies, comparing pre-treatment numbers with those 1-2 years following habitat modification or disturbance. Such short temporal scales may not reveal actual responses of birds to habitat modification, given that considerable time lags may exist (Hagan et al. 1996).

Some studies have evaluated habitat quality over a range of different habitats by comparing reproductive success (Vickery et al. 1992b, Delisle and Savidge 1996, Purcell and Verner 1996, Powell and Collier 1998, Rangen et al. 2000), or male pairing success (Villard et al. 1993, Hunt 1996). Pairing success or reproductive success may provide the most meaningful and direct information regarding habitat quality, as both should be maximised in highest quality habitat (Hunt 1996). In addition to reproductive success, reductions in habitat quality may be expressed in other ways, and measured using other indices.

Body condition of breeding birds may be a strong correlate of available food, and thus a good indicator of habitat quality. Poor body condition may limit reproduction and reduce survival in birds (Martin 1987, Arcese and Smith 1988, O'Halloran et al. 1990, Selman and Houston 1996, Haas 1998). For White-throated Sparrows, males with high relative body condition had higher rates of reproductive success than individuals in poor body condition (Chapter 2).

The purpose of this study was to determine if habitat quality for the White-throated Sparrow differed between recent clearcuts, edges, and interior forest habitats in a boreal forest landscape. I chose the White-throated Sparrow because it is generally considered a habitat generalist (Westworth and Telfer 1993, Scheick 1995, Darveau et al. 1995, Rail et al. 1997, Schmiegelow et al. 1997, Song 1998) and is known to establish

territories and attempt to breed in recent clearcuts (Darveau 1997, Schmiegelow et al. 1997). Despite this, significant Canada-wide declines (1.1%/yr) in White-throated Sparrow's on Breeding Bird Surveys (BBS), have occurred between 1966 – 1996 (Downes et al. 1999).

I assessed habitat quality for White-throated Sparrow's, in a fragmented habitat matrix 5-6 years following forest harvesting, through measurement of reproductive success (actual nests and use of a reproductive index method), male pairing success, and body condition (proportional body condition). I used these indices to assess whether forest harvest and fragmentation affected habitat quality for the White-throated Sparrow. I studied three habitat types: edges, clearcuts, and interior forest. If White-throated Sparrows are not impacted by forest harvest and fragmentation, then:

(1) Territory density should not differ between habitat types.

(2) Body condition of birds should not differ between habitat types.

(3) Reproductive success and pairing success should not differ between habitat types.

3.2 Methods

3.2.1 - *Study Area*

This study was conducted the mixed-wood boreal forest near Calling Lake, Alberta (55°15'N, 113°19'W) in 1998 and 1999 (see Chapter 2).

3.2.2 - *Bird Territory Density*

I used spot-mapping to determine White-throated Sparrow density (Robbins 1970), conducting twelve census 'rounds' from 16 May to 23 July in 1998, and sixteen

census 'rounds' from 2 May to 25 July in 1999. Plots were spatially referenced using a 50 X 50 m grid, permitting ready identification of points on survey sheets. I censused each plot every 2-7 days during the breeding season. To reduce potential sampling biases, I alternated observers and start locations for each plot, on each census round. I began each census at dawn and continued for a maximum of five hours, to ensure sampling was conducted during the peak hours of male territorial singing. A census was halted in high winds or in the event of measurable precipitation. A bird was considered territorial if it was detected singing in the same area for a period of at least ten days, was paired, or showed any evidence of nesting (Robbins 1970). Only those territories with greater than fifty percent of mapped locations occurring within the plot were included in analyses. Territories that bordered the clearcut/edge interface were assigned to a particular treatment if greater than fifty percent of detections occurred in that treatment.

3.2.3 - *Body Condition*

I captured White-throated Sparrows in mist nets using song playbacks. Each captured bird was given a unique combination of 2 (1998), or 3 (1999) coloured plastic leg bands and one U. S. Fish and Wildlife Service aluminium band. For each captured bird I determined sex through a combination of wing length and presence of brood patch or cloacal protuberance (Pyle et al. 1997). I was unable to confidently determine the age of second year birds by colour differences in coverts or the wear and shape of rectrices, as described by Pyle et al. (1997). Using this method, several recaptured birds known to be at least in their third year had plumage indicative of birds in their second year. I measured wing length to the nearest millimetre using unflattened wing chord, and body

mass to the nearest gram using a 50 g Pesola spring balance. I estimated the body condition of birds using the ratio of body mass to wing chord length (Winker et al. 1992).

3.2.4 - *Reproductive Success*

I measured reproductive success through a combination of locating and monitoring White-throated Sparrow nests and through the use of a reproductive index (Vickery et al. 1992a). Territories were ranked on a scale from 1 to 5, on the basis of behavioural cues with increasing evidence of reproductive success (see Table 2.1). Territories which produced ≥ 1 fledgling (high success) were assigned a rank of 5, whereas territories which produced no fledglings (low success) were assigned a rank from 1 to 4, depending on observations of other reproductive cues. In 1999, I also measured reproductive success using a standardised search effort (hereafter called the 'search' technique). After six spot-mapping census rounds, I roughly delineated the boundaries of all territories. I then located the approximate centre of the territory on the alphanumeric grids within each plot and systematically searched each territory for breeding evidence. I began each search effort at the territory centre, walking lines in 5 m increments radiating outwards towards the territory boundary. I searched each territory for 15 minutes, whether I managed to detect a territorial bird or not. If I located a territorial individual, I followed the bird until 15 minutes had elapsed, and recorded all reproductive behaviour. I ended the survey before 15 minutes if I detected ≥ 1 fledgling. Timing of these surveys was based on the chronology of reproductive activity as measured by actual White-throated Sparrow nests. Each territory was surveyed twice, exactly ten days apart, between 28 June and 10 July. Only territories which fulfilled the

≥ 4 week occupancy requirement specified by Vickery et al. (1992a) were used for analysis.

3.2.5 - *Statistical Analysis*

All proportional data were arcsine $\sqrt{p}$ transformed prior to analysis, where p represents a proportion (Zar 1996). A Kolmogorov-Smirnov goodness of fit test with Lillefors correction was used to examine the normality of both my dependent and independent variables. I tested for homogeneity of variances using Levene's test (SPSS 1999). I tested for differences between years in my habitat quality indices (independent variables) using t – tests. I conducted post-hoc power analyses using the program GPOWER (Faul and Ehrdfelder 1992), on non-significant results.

I compared bird density between habitats for both years combined using a one-way ANOVA. I compared observer effort in each treatment by dividing the total amount of time spent (in minutes) in each plot during the entire season by the territory density of that plot. This gave an indication of the survey effort on a territory basis, instead of total time spent within each habitat treatment. Effort (based on density) between habitats and between years was compared using a two-way ANOVA.

I compared body condition (dependent variable) between habitats, years and between sexes (independent variables), with time of day and date as covariates, using Analysis of Covariance (ANCOVA). I included sex, time of day and date in this model, as Falls and Kopachena (1994) suggest that these could be significant factors contributing to differences in the body mass of White-throated Sparrows.

I compared reproductive success for White-throated Sparrow nests in a 3 X 2 contingency table using a randomised G-test, based on 10, 000 randomisations. I

compared overall mean reproductive indices and reproductive success (rank 5), between habitats using one-way ANOVA. I compared the two reproductive indexing methods used in 1999 using a *t*-test, and compared each index method independently between habitats using one-way ANOVA.

In all analyses, I considered an alpha ≤ 0.05 to be highly significant and an alpha ≤ 0.10 to be marginally significant. Following a significant ANOVA result, I used Bonferroni post hoc multiple comparisons to test for differences among individual treatments. All data are presented as mean ± SE. All analyses were performed using SPSS (Version 10.0) (SPSS 1999).

3.3 - Results

3.3.1 - *Bird Territory Density*

Average White-throated Sparrow territory density did not differ significantly between years (*t* - test, $t = 0.97$, $df = 1$, $p = 0.35$), with a mean density of 13.78 ± 1.22 per plot in 1998 (n=123), and 11.89 ± 1.52 per plot in 1999 (n=107)(Figure 3.1). Across years, territory density did not differ significantly between habitat treatments, as predicted (one-way ANOVA, $F = 3.33$, $df = 2$, $P = 0.11$). Power to detect this difference was 42%.

3.3.2 - *Body Condition*

The body condition of birds did not vary between years, so all comparisons were made with average body condition over both years (Table 3.1). Body condition of birds did not differ between habitat types ($p = 0.54$; Table 3.1), with power to detect difference at 15%. Body condition of females was consistently higher than that of males (females, 0.368 ± 0.004 g/mm; males 0.358 ± 0.002 g/mm; $p = 0.003$; Table 3.1). Date was a

significant covariate, with birds starting the season in poorer condition than that achieved later in the season.

3.3.3 - *Reproductive Success*

A total of 31 White-throated Sparrow nests were located in 1998 and 1999. Of these, only 8 successfully fledged young (25.8% success); 3 of 17 (17.6%) were successful in edge habitat, 5 of 12 (41.7%) in interior forest, and 0 of 2 (0%) in clearcuts (Table 3.2). There was no significant difference in number of successful nests between habitats, with both years combined (G-test; $\chi^2 = 2.07$, df = 2, $p = 0.36$), although sample sizes were small. All nests were located prior to, or during incubation. Of the nests that were depredated, most were during the nestling stage (19 of 24, 79%), with fewer taken during the incubation stage (5 of 24, 21%).

Using the method of Vickery et al. (1992a), I also calculated reproductive indices for 204 territories (106 in 1998, 98 in 1999) (Table 3.2). Reproductive indices were not significantly different between years (t - test, $t = 1.36$, df = 1, $P = 0.19$). Contrary to my prediction, overall mean reproductive rank was significantly different between habitats (one-way ANOVA, $F = 7.11$, df = 2, $p \leq 0.01$; Figure 3.2). In post-hoc multiple comparisons, overall mean reproductive rank was significantly higher in interior forest than in clearcut ($p = 0.03$), however differences were not significant between edge and clearcut ($p = 0.20$), or between edge and interior forest ($p = 0.45$). Across all habitats, a total of 71 territories (34.8%) had a rank of 5 (successful in fledging ≥ 1 young). Thirty territories (34%) had a rank of 5 or higher in edge habitat, 10 territories (21%) in clearcuts, and 31 territories (46%) in interior forest. The proportion of territories achieving a rank of 5 (fledging success) was significantly different between habitats (one-

way ANOVA; $F = 4.63$, $df = 2$, $p = 0.03$). In post-hoc multiple comparisons, reproductive success was marginally higher in interior forest than clearcuts ($p = 0.08$), however differences were not significant between edge and clearcut ($p = 0.20$), or between edge and interior forest ($p = 0.55$; Figure 3.3). Overall, proportional pairing success was 65.3 ± 4.97 % in edge habitat, 38.2 ± 7.37 % in clearcuts, and 76.8 ± 3.94 % in interior forest. The proportion of territories in which males were paired was also significantly different between habitats (one-way ANOVA; $F = 13.55$, $df = 2$, $p \leq 0.01$). In post-hoc multiple comparisons, pairing success was higher in interior forest than clearcuts ($p = 0.01$), and higher in edge than clearcut ($p = 0.04$), however differences were not significant between edge and interior forest ($p = 0.45$).

Since the Vickery et al. (1992a) reproductive index method depends on observational data, it is important to standardise survey effort between habitat treatments if consistent comparisons are to be made. Survey effort was significantly greater in 1999 than 1998 (t - test; $t = 19.0$, df = 1, $p = 0.02$), however, there was no significant difference in survey effort between habitats in either 1998 (one-way ANOVA; $F = 0.84$, $df = 2$, $p = 0.48$), or 1999 (one-way ANOVA; $F = 1.56$, $df = 2$, $p = 0.28$). However, power to detect differences was low at 14% in 1998, and 21 % in 1999.

In 1999, I also determined reproductive ranks using the 'search' method, in order to standardise search effort. By comparison, the 'search' method produced a higher mean overall reproductive rank (2.83 ± 0.18), than did the Vickery et al. (1992a) method (2.66 ± 0.18). However, there was no significant overall difference between methods (ANOVA, $F = 0.59$, df = 1, $p = 0.45$; Figure 3.4), or in the interaction between method

and habitat type (ANOVA, $F = 0.21$, $df = 2$, $p = 0.81$), based on reproductive indices in 1999. Power to detect these differences was 12 % and 8 %, respectively.

The definition of what constitutes a territory using the spot-mapping method requires the observation of a male for a period of only 10 days (Robbins 1970) whereas the reproductive index method requires 4 weeks (Vickery et al. 1992a). Given these differences in the period of occupancy, several territories classified using Robbins (1970), were abandoned prior to being included as a potential breeding territory using Vickery et al. (1992a). Interestingly, there was considerable difference between habitat treatments in the number of territories included in analyses using each method. For both years combined, fewer territories were abandoned after 4 weeks in interior forest habitats (68 vs. 70, 3% difference), than in edge habitat (88 vs. 98, 10 % difference), or in clearcuts (48 vs. 63, 24% difference). However, the number of territories that were present at 10 days and were still occupied at 4 weeks was not significantly different between habitat types (G-test; $\chi^2 = 1.70$, df = 2, $P = 0.43$) (Figure 3.5).

3.4 – Discussion

I made three predictions about habitat quality indices across three habitat types in a recently harvested and patchy landscape, based on a null hypothesis that White-throated Sparrows were not impacted by forest harvest: 1) that territory density should not differ among habitat types; 2) that the body condition of birds should not differ among habitat types; and 3) that reproductive success should not differ among habitat types. My results were consistent with predictions 1 and 2, but were inconsistent with prediction 3. Both pairing success (rank 2) and reproductive success (rank 5) differed significantly between

habitat types, however, proportional male body condition was not significantly different. Interior forest and edge habitats had significantly higher reproductive success and pairing success than clearcuts.

3.4.1 - *Density across habitat types*

These results suggest that if fragmentation is reducing habitat quality for White-throated Sparrows in the boreal mixed-wood forest of central Alberta, density provides a poor measure. In this study, variation in White-throated Sparrow territory density was best explained by patterns in the amount of canopy cover (K. Hannah, unpubl. data). This result is consistent with Falls and Kopachena (1994), who found that White-throated Sparrows favour forests with low canopy cover. Harper (1999) found that the creation of edge in boreal mixed-wood forests led to increased tree mortality and snag breakage, thereby reducing canopy cover. Cumming et al. (2000), found that the size of canopy gaps in aspen forests, such as those used in this study, increased linearly as a function of stand age, also leading to reductions in canopy cover. In the 5-6 year old clearcuts used in this study, canopy closure was extremely low, except in small patches of residual standing trees. High variability in both the structure and canopy cover of these forests, among habitat treatments, may be responsible for the lack of significant differences in the territory density of White-throated Sparrows in this study.

White-throated Sparrows were very abundant in my study area, and territory density may have reached reach saturation in the best quality habitat. Individuals may then be forced to settle into vacant territories in surrounding, low quality habitat to maximise individual fitness (Fretwell and Lucas 1970), thus territory density may not reveal potential differences in habitat quality. In a recent study conducted about 350 km

west of my study site, male White-throated Sparrows settled in young forests (25 years old), but at much lower density than old forests (75-100 yr.) (Rangen et al. 2000). Young forests (25 – 30 yr) may be poor quality habitat within this matrix, such that territorial male White-throated Sparrows avoid them. The use of clearcuts (5-6 year old forest) in my study area suggests that this habitat may be more suitable than older, regenerating forests, to White-throated Sparrows. However, as clearcuts regenerate, the canopy closes, and the suitability of young forest may decrease over time. Therefore, determining the temporal suitability of regenerating clearcuts to this species would be beneficial to its management, given the dynamic nature of the landscape matrix.

3.4.2 - *Body condition*

Differences in the body condition of birds within a fragmented forest matrix may be apparent, provided differences exist in some habitat attribute (e.g. food abundance, competition). In European dippers (*Cinclus cinclus*) the body condition of birds in acidic streams was poorer than those on circumneutral streams (O'Halloran et al. 1990, Omerod and Tyler 1990), indicating that differences in habitat quality can directly affect the condition of birds. Numerous studies have implicated food supply or food quality as the cause for reduced reproductive success (Högstedt 1981, Arcese and Smith 1988, Dhindsa and Boag 1990, Komdeur 1996). Male body condition was related to reproductive success in plots of differing density (Chapter 2), however, among the three habitat treatments in this study, male body condition was not related to reproductive success. At this scale, reduced reproductive success may be a result of differences in predation or individual fitness and not male body condition.

Time of year and sex were significant predictors of proportional body condition in this study, as in other studies (Omerod and Tyler 1990, Tuttle 1993). Birds arriving from migration in spring tend to be in poorer condition, so increases would be expected following arrival on the breeding grounds, as more plentiful food sources become available. Females also have more time to forage than males, without having to engage in territorial singing, and amass fat reserves prior to egg-laying (Tuttle 1993).

3.4.3 - *Reproductive success across habitat types*

I failed to detect any significant differences in nest success between habitat types given the small sample of White-throated Sparrow nests located. Overall success of White-throated Sparrow nests in this study was 25.8%, slightly below the minimum of 30.0 % nest success recorded for this species in other areas (Falls and Kopachena 1994). It is possible that the nests I located were a non-random sample, and also more conspicuous to predators (Vickery et al. 1992c). It is also possible that either my presence at these nests, or human scent associated with my presence, may have been a factor, although I attempted to minimise my presence and vary my route when approaching and leaving nests. In addition, empirical evidence suggests that the presence of human observers and scent at nest sites has little or no influence on rates of nest predation (Hoi and Winkler 1994, Mayer et al. 1997).

Murid rodents appeared to be responsible for the majority of depredation during the incubation stage, as most predated nests contained shell fragments with small tooth marks (K. Hannah, unpubl. data, see also Tittler and Hannon 2000). Although I never observed a predation event at a White-throated Sparrow nest, the probable predators of nestlings would be red squirrels (*Tamiasciurus hudsonicus*), short-tailed weasels

(*Mustela erminea*). In one instance, there was evidence of a black bear (*Ursus americanus*) depredating a nest. I suspect short-tailed weasels depredated nests in two instances, as I also located the remains of brooding females near the nest. Avian predation was probably low, given the nature of observed predation events and the low relative abundance of corvids in the study area (Cotterill and Hannon 1999, Schmiegelow et al. 1997, Tittler and Hannon 2000).

In recent years, numerous nest predation studies involving the use of artificial nests have been conducted in fragmented areas surrounding my study site (< 100 km radius) (Cotterill and Hannon 1999, Song and Hannon 1999, Tittler and Hannon 2000). Results of these studies consistently show no effect of edge on increased rates of nest predation. However, the use of artificial nests to evaluate nest predation has been heavily criticised in recent years (Roper 1992, Haskell 1995a and 1995b, Wilson and Brittingham 1998). Given that the majority of predation events in this study occurred during the nestling stage, studies measuring rates of egg predation may not accurately reflect actual predation rates. The index method of Vickery et al. (1992a), provides no direct evidence of predation, as it simply assesses whether a territory successfully produces young. Although predation may be the mechanism for reduced reproductive success, without evidence of increased predation from monitored nests in any one habitat type, I cannot implicate nest predation as the cause of reduced reproductive success in my study.

Instead of increased predation causing reduced reproductive success in different habitats, a combination of reduced pairing success, lower male body condition, and increased competition may result in reduced fitness in different habitats. Ovenbird (*Seiurus aurocapillus*) females are able to recognise and avoid inferior habitat (Gibbs and

Faaborg 1990, Villard et al. 1993), thereby reducing the pairing success of males in poor quality habitat; in the case of my study, clearcuts. Males may not be able to discriminate inferior habitat, as they settle territories prior to leaf-out, and may occupy habitats at densities that do not reflect their future quality (Hagan et al. 1996). Pairing success of male White-throated Sparrows in my study was 42% in clearcuts, 65% in edge habitat, and 78% in interior forest. These results suggest that female White-throated Sparrows are better able to assess habitat quality than males. Since they arrive an average of 14 days after males (K. Hannah unpubl. data), females may have a better opportunity to assess habitat quality prior to settling. Four females in edge habitat, and a single female in interior forest, mated polygynously with paired males rather than pairing with unmated males in clearcuts or potentially poor quality males in edge and interior forest habitat (K. Hannah unpubl. data). Rates of pairing success mirrored both male fat scores, and rates of reproductive success for White-throated Sparrows in this forest matrix, with 21% of territories fledging at least one juvenile in clearcuts, 34% in edge habitat, and 46% in interior forest.

Based on my results, clearcuts appear to represent poor quality habitat for White-throated Sparrows in my study area. Interior forest, on the other hand, appears to represent high quality habitat, based on mean reproductive success. Edges may also represent quality habitat, as high territory densities offset lower average reproductive success, resulting in similar potential rates of recruitment as those in interior forest habitat. I cannot assess the potential source/sink dynamics of the habitats that I studied, as I did not calculate demographic parameters, such as fitness and survival, essential for such comparisons (Pulliam 1988). However, the consistently poor reproductive success

in clearcuts during this study, relative to other habitats, suggests that this habitat probably functions as a reproductive sink.

3.4.4 - *Territory abandonment*

The two methods I used for determining territory occupancy (Robbins 1970, Vickery et al. 1992a) resulted in different numbers of occupied territories in different habitats. The method of Robbins (1970) confirms territoriality if a male is present in the same location for ≥ 10 days, whereas Vickery et al. (1992a) confirms territoriality for the purposes of breeding if a male is present ≥ 4 weeks. In clearcuts, only 76% of territories occupied after 10 days were still occupied after 4 weeks; in edge, 90%, and in interior forest, 97%. This suggests that more territories in clearcuts were abandoned prior to nesting than in either edge habitat or interior forest. Two plausible explanations for such differences involve dispersal or mortality of territorial birds. I have little data to support hypotheses about adult mortality rates. Observations of Merlin (*Falco columbarius*), and American Kestrel (*Falco sparverius*) were made in clearcuts, whereas observations of Sharp-shinned Hawk (*Accipiter striatus*), Northern Goshawk (*Accipiter gentilis*), and Broad-winged Hawk (*Buteo platypterus*) were made predominately within forest (K. Hannah unpubl. data). Given the presence of these predatory hawks across all habitats, rates of adult mortality may be similar, however, certain species may depredate passerine birds more efficiently than others. Territorial birds may disperse prior to nesting for several reasons: 1) males fail to attract a mate and disperse to look elsewhere; 2) males attract mates, but behavioural incompatibility prevents nesting; 3) males attract mates, but competition and intrusion pressure force birds to disperse. The patterns reflected in rates of male pairing success between habitats would support hypotheses 1 and 3. After

establishing and defending a territory, males which fail to acquire mates may disperse after a period of time, in an attempt to locate more suitable territories and potential mates elsewhere. Males in low quality habitats, where the majority of males are unpaired, may also disperse due to competition and intrusion pressure from neighbouring, unpaired birds.

3.4.5 - *Age-specific demography*

Given my inability to differentiate the age of White-throated Sparrows effectively, I was unable to assess whether there were any age-specific demographic differences between individuals in different habitats. Age-specific demographic data may explain differences in habitat quality beyond the scope of simple density or abundance data (Fretwell and Lucas 1970, Van Horne 1983). Bollinger and Gavin (1989) explained most differences in reproductive success and reproductive output between habitats using such data, with younger, inexperienced birds consistently occupying poorer quality habitat and producing fewer offspring. Having good age-specific morphological information would have enhanced this study, and therefore, should be a priority in future White-throated Sparrow banding studies.

3.4.6 - *Conclusions and Management Recommendations*

Density provided a poor measure of habitat quality and was an unreliable means of assessing the effects of forest harvest and fragmentation on the population of White-throated Sparrows I studied. Clearcuts were consistently shown to be poor quality habitat for this species, with respect to reproductive success, body condition, and trends in behavioural time-budgets. Edge and interior forest represented higher quality habitat. Future research on the White-throated Sparrow and similar habitat generalists must

incorporate indices beyond simple measures of density or abundance. Developing more efficient ways of censusing female passerines may also provide more meaningful data with respect to species conservation and management.

While data on reproductive success is both logistically difficult and time-consuming to collect, and may not be an effective means of evaluating habitat quality for multiple species, evidence of pairing success may provide a more meaningful and time-efficient measure of actual habitat quality (Villard et al. 1993, Hunt 1996, see Chapter 2). Data of this nature will help to promote a better understanding of the impacts of forest harvest and fragmentation on passerine birds in the boreal mixed-wood forest of central Alberta.

Emphasis on nest predation in future research needs to be critically evaluated in the context of the geographical location of the study and the intended goals of the research. In the boreal mixed-wood forest of central Alberta, predation rates may not be exacerbated by the creation of edge. The absence of opportunistic predators such as raccoons (*Procyon lotor*), and striped skunks (*Mephitus mephitus*), and the low density of corvids (especially crows, jays, and magpies), probably lessen the risk of increased predation associated with the creation of edge that has been documented in other studies throughout North America (Gates and Gysel 1978, Brittingham and Temple 1983, Gates and Giffen 1991). However, future predation studies in this region should extend beyong the egg stage, as most predation I documented occurred at the nestling stage.

Although I studied only the White-throated Sparrow, several other habitat generalist species, such as Yellow Warbler (*Dendroica petechia*), Tennessee Warbler (*Vermivora peregrina*), Mourning Warbler (*Oporornis philadelphia*), Lincoln's Sparrow

(*Melospiza lincolnii*), and Chipping Sparrow (*Spizella passerina*), may exhibit similar patterns of response. Population-level work on any of these species would be beneficial in determining whether the patterns observed in White-throated Sparrows are consistent with other species with similar patterns of habitat use. In addition, research conducted at a number of successional stages, from harvest to maturation, would be useful in determining the temporal nature of habitat quality.

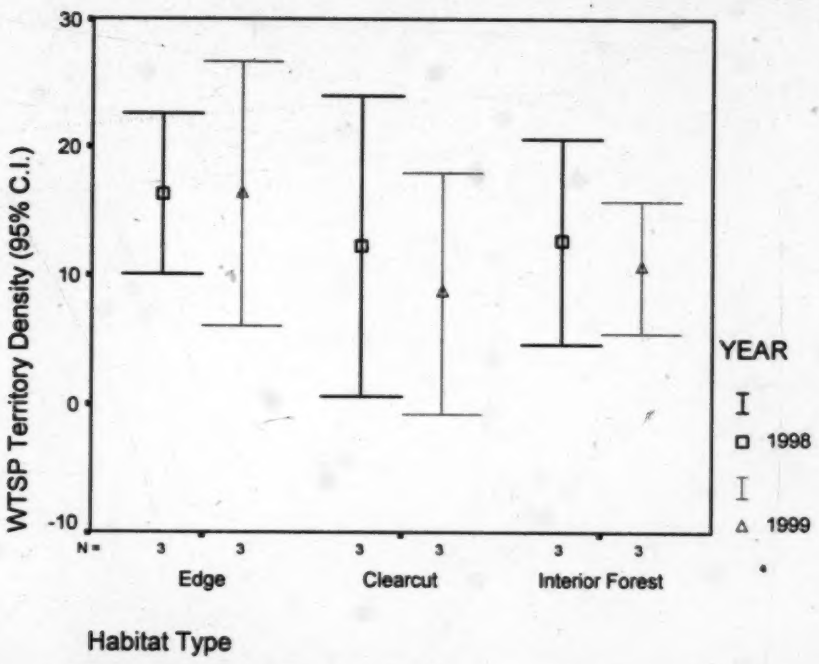

Figure 3.1 – Territory density (mean ± SE) of White-throated Sparrows in edge, clearcut, and interior forest habitats in 1998 and 1999.

Source	*df*	F	*p*	Power
Time	1	0.006	0.94	0.05
Date	1	6.15	0.02	0.69
Year	1	2.79	0.1	0.38
Sex	1	9.29	0.003	0.86
Habitat	2	0.62	0.54	0.15
Year*Sex	1	0.02	0.89	0.05
Year*Habitat	2	0.23	0.79	0.09
Sex*Habitat	2	0.34	0.72	0.1
Year*Sex*Habitat	2	0.11	0.89	0.07

Table 3.1 – Results of analysis of covariance (ANCOVA) on proportional body condition, with year, sex, and habitat as independent variables, and time of day and date as covariates. Power estimates are post-hoc and represent actual power to detect differences for each variable or interaction. An alpha of 0.05 was considered significant, and an alpha between 0.05 and 0.10 was considered marginally significant.

	Edge	Clearcut	Interior Forest	Total
Territories (n)	88	48	68	204
Rank 5	30	10	31	71
Rank 5 (%)	34.1	20.8	45.6	34.8
Nests (n)	17	2	12	31
Nest success (n)	3	0	5	8
Nest success (%)	17.7	0	41.7	25.8

Table 3.2 – Summary of reproductive success from actual monitored nests and from Vickery et al. (1992a) reproductive rankings for 1998 and 1999 combined. Rank 5 represents territories which produced ≥ 1 fledgling.

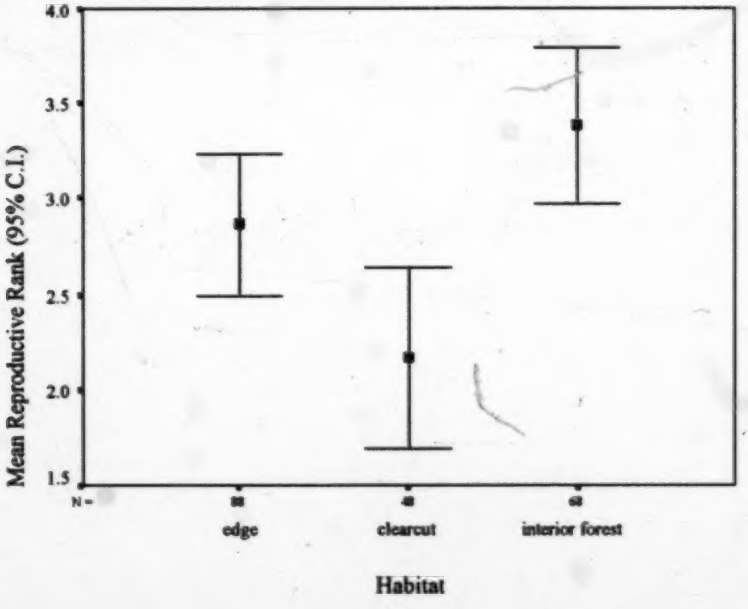

Figure 3.2 – Comparison of mean reproductive rank for edge, clearcut and interior forest habitats for 1998 and 1999 combined.

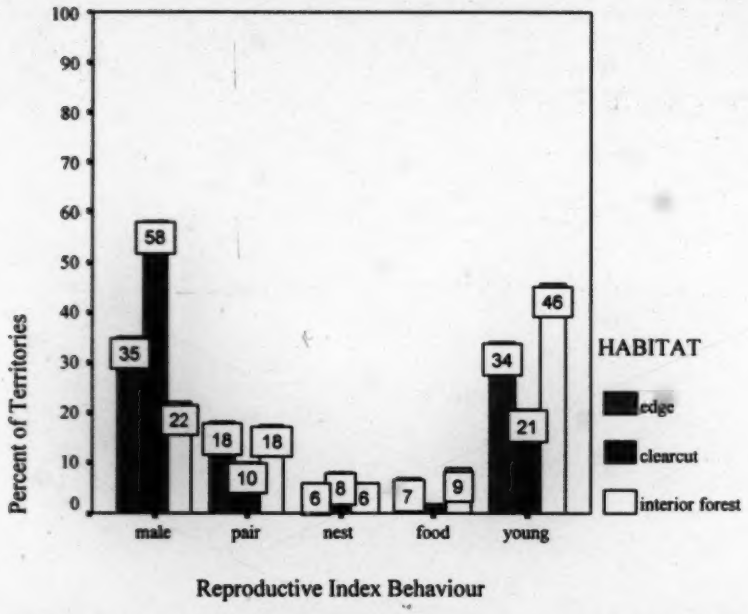

Figure 3.3 – Summary of maximum breeding ranks (Vickery et al. 1992b) for territories in edge, clearcut, and interior forest habitat in 1998 and 1999. Values represent the number of territories for which a specific behaviour was the maximum recorded.

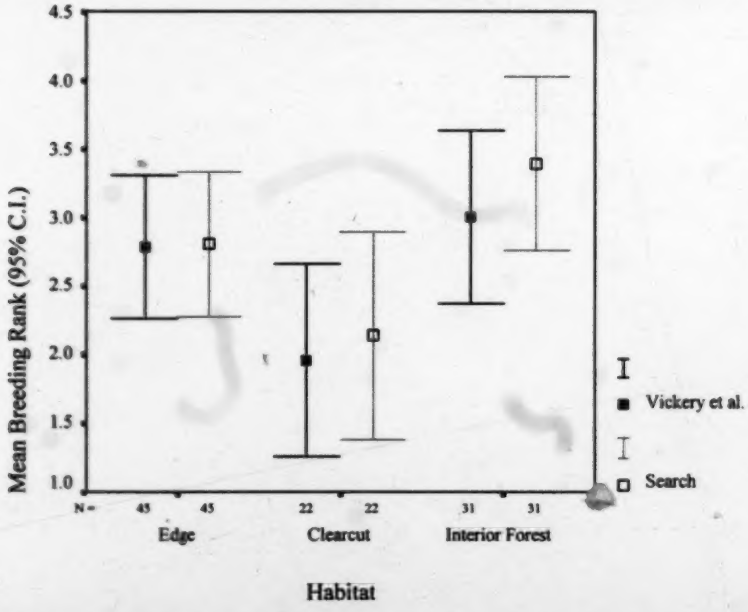

Figure 3.4 – Comparison of mean reproductive ranks for edge, clearcut , and interior forest habitats using Vickery et al. (1992a) method and 'search' method in 1999.

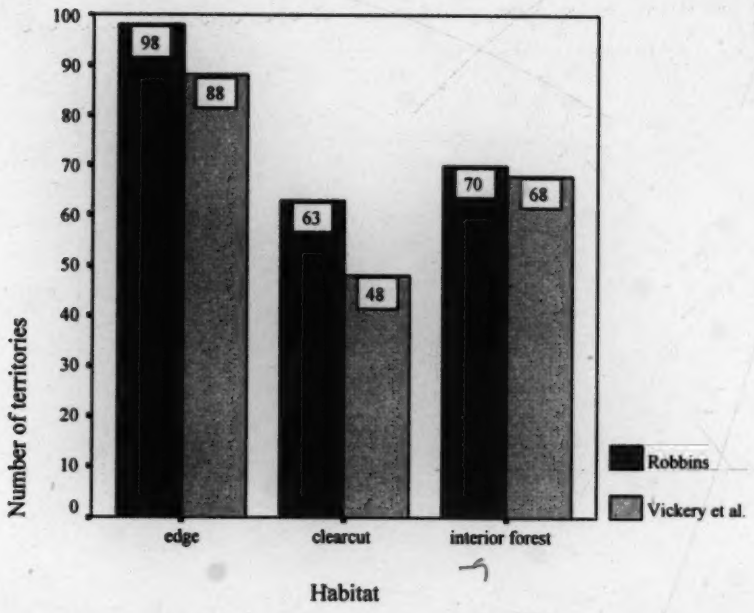

Figure 3.5 – Number of territories occupied after 10 days (Robbins 1970) vs. number of territories occupied after 4 weeks (Vickery et al. 1992a) in edge, clearcut, and interior forest habitats for 1998 and 1999.

3.5 - Literature cited

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CHAPTER 4 – THE ROLE OF HABITAT QUALITY ON BREEDING CHRONOLOGY, SITE FIDELITY, AND DISPERSAL IN THE WHITE-THROATED SPARROW.

4.1 - Introduction

Natural selection should favour individuals capable of accurately assessing habitat quality on the breeding grounds (Lanyon and Thompson 1986), through improved fitness, survival, or both. The adaptive significance of this has been demonstrated in male passerines settling in high quality habitat first (Brown 1969, Alatalo et al. 1984, Lanyon and Thompson 1986, Arcese 1987, Bensch and Hasselquist 1991, Aebischer et al. 1996), exhibiting higher rates of site fidelity in high quality habitat (Baeyens 1981, Newton and Marquiss 1982, Bollinger and Gavin 1989, Hatchwell et al. 1996), and dispersing shorter distances from previous breeding sites in high quality habitat (Harvey et al. 1979, Dow and Fredga 1983, Weatherhead and Boak 1986, Jakobsson 1988). Further, birds that occupy a poor quality site in one year will often move to better quality habitat in the following year (Bollinger and Gavin 1989, Matthysen et al. 1995). Site fidelity could also be advantageous to the individual if familiarity with a site improves foraging efficiency or predator avoidance (Hinde 1956).

Some empirical studies suggest reproductive success is a strong correlate of site fidelity and dispersal distance in male birds (Gratto et al. 1985, Jakobsson 1988, Gavin and Bollinger 1988, Haas 1990, 1998). However, others suggest the overall nesting success of birds at a particular site, and not individual success, acts as a strong determinant of site fidelity (Cadion et al. 1993, Haas 1997). Nevertheless, these associations are not always observed: birds sometimes return to poor quality habitat,

despite vacancies in nearby better quality habitat (Lanyon and Thompson 1986), or return for several years to habitats which have deteriorated in quality (Hildén 1965, Wiens and Rotenberry 1986). This is especially true in highly fragmented landscapes where breeding habitat may be limited or isolated, and alternate sites are far away (Haig and Oring 1988, Matthysen et al. 1995).

In general, patterns of site fidelity, mortality, and dispersal differ between sexes, with females typically dispersing greater distances between years than males (Greenwood 1980, Breitwisch 1989, Ens et al. 1993, Falls and Kopachena 1994, Orell et al. 1994, Part 1995). Females may disperse as a result of mate incompatibility, to avoid incestuous matings, or to improve mate/territory quality, all of which result in low rates of breeding site fidelity (Gratto et al. 1985, Payne and Payne 1993, Dhondt and Adriaensen 1994, Murphy 1996). This suggests that females may be better able to assess habitat quality prior to settlement than males (Probst and Hayes 1987, Sherry and Holmes 1989, Smith and Arcese 1989, Gibbs and Faaborg 1990, Holmes et al. 1992). The result of such female-based selection can be reduced pairing success of males in poor quality habitat (Villard et al. 1992, Hagan et al. 1996, Hunt 1996).

I studied a population of White-throated Sparrows (*Zonotrichia albicollis*) in a fragmented landscape between 1998 and 2000. The White-throated Sparrow is a large, conspicuous, and highly abundant passerine species, common throughout the western boreal forest (Falls and Kopachena 1994, Hyslop and Kennedy 1996). White-throated Sparrows are typically monogamous and may exhibit sex-specific differences in site fidelity, dispersal and mortality (Lowther and Falls 1968, Knapton et al. 1984). The purpose of this study was, first, to assess whether differences existed in the breeding

chronology, site fidelity, and dispersal of male and female White-throated Sparrows. Second, I wanted to evaluate these variables across three broad habitat types (interior forest, recent clearcuts, and forest/clearcut edges) known to differ in terms of quality (see Chapter 3), and to identify the mechanism(s) responsible for these patterns. Both reproductive success and pairing success were highest in interior forest habitat (Chapter 3). Therefore, I predicted that interior forest habitat should be settled first, should have the highest rates of site fidelity, and should have the lowest dispersal distances for both males and females between years. As well, since rates of fidelity and dispersal are known to differ between male and female White-throated Sparrows (Falls and Kopachena 1994), I wanted to investigate whether the mechanisms determining occupancy, fidelity, and dispersal were different between sexes.

4.2 - Methods

4.2.1 - *Study area*

This study was conducted the mixed-wood boreal forest near Calling Lake, Alberta (55°15'N, 113°19'W) in 1998 and 1999 (see Chapter 2).

4.2.2 - *Capture, marking, and body condition*

In 1998 and 1999, I captured a total of 86 male and 37 female White-throated Sparrows in mist nets using audio playback of recorded song. Each captured bird was given a unique combination of 2 (1998), or 3 (1999) coloured plastic leg bands and one U. S. Fish and Wildlife Service aluminium band. I determined the sex of each captured bird through a combination of wing length and presence of brood patch or cloacal protuberance (Pyle et al. 1997). I measured wing length using unflattened wing chord, and body mass using a 50 g Pesola spring balance. I estimated the body condition of

birds using the ratio of body mass (g) to wing chord length (mm)(Winker et al. 1992) and interclavicular fat scores (Haas 1998). Fat was scored on a scale from 0 (no visible fat) to 2 (fat filling the cavity) at intervals of 0.5.

4.2.3 - *Reproductive success and pairing success*

I measured reproductive success through the use of a reproductive index method (Vickery et al. 1992). Territories were ranked on a scale from 1 to 5 on the basis of behavioural cues with increasing evidence of reproductive success (Table 2.1, Chapter 2). Territories which produced ≥ 1 fledgling (high success) were assigned a rank of 5, whereas territories which produced no fledglings (low success) were assigned a rank from 1 to 4, depending on observations of other reproductive cues.

4.2.4 - *Determination of breeding chronology*

For the purposes of this study, breeding chronology was described by the date of initial territory settlement, the date when a pair was first observed on a territory, and finally, the date when fledgling(s) were observed on territory. These three measures covered the entire breeding chronology for this species, thus accurately assessing habitat quality. Individuals in high quality habitat should establish territories first, acquire mates first, and produce young sooner than in other habitats. This strategy should confer the greatest evolutionary advantage, especially for a species that is known to double-brood (Knapton et al. 1984, Kopachena 1992), and occasionally triple-brood (Loncke and Falls 1973). The date of pairing represents the arrival chronology of female White-throated Sparrows, since they typically arrive later than males (Falls and Kopachena 1994).

The breeding chronology of individuals between habitats was compared using the date I first detected an individual on territory, the date of female arrival on a male's

territory, and the date I first recorded the presence of ≥ 1 fledgling on an individual territory. Only those territories known to be occupied by a singing male for a minimum of 10 days (Robbins 1970), were included in analyses. Since I initiated surveys late in the spring of 1998 and finished early in the summer of 2000, not all stages of the breeding chronology could be compared between all years. Therefore, comparisons in the patterns of initial settlement were made only for data collected in 1999 and 2000. For mean date of pairing and mean first date when young were observed on territory, I used data collected in 1998 and 1999. Since comparisons of each aspect of the breeding chronology were made between different years and were also highly variable, habitat comparisons were made for each aspect of the breeding chronology, for each year, individually.

4.2.5 - *Site fidelity*

Individuals colour marked in the previous breeding season were relocated in the following year using spot-mapping (Robbins 1970). In 1999, 16 spot-mapping census 'rounds' were conducted throughout the entire breeding season; in 2000, 10 census 'rounds' were conducted during the month of May. Only individuals that returned to the same 10 ha plot where they had established a territory in the previous year were included in estimates of site fidelity. Given that the distances between plots was variable, birds that dispersed outside the plot from which they were initially territorial were not included in analyses. Individuals considered to be non-territorial (transients or floaters) in the previous breeding season were also excluded from analysis.

4.2.6 - *Estimation of Dispersal Distances*

I calculated dispersal distances for individual birds by measuring the distance between the centre of an individuals territory between year *t* and year *t*+1. Territories were delineated by mapping locations of territorial birds using spot-mapping (Robbins 1970). A cluster of points within an alphanumeric grid typically represented the territory of an individual. Although this represents a coarse estimate, I feel it is a reasonable measure, given that male activity in the White-throated Sparrow is generally concentrated towards the territory centre (Falls and Kopachena 1994). Dispersal distances were then measured to the nearest metre on 1:20 000 grid sheets.

4.2.7 - *Statistical Analyses*

I compared differences in mean dates in the breeding chronology among habitat treatments using either one-way analysis of variance (ANOVA) or Kruskal-Wallis (ANOVA), after initial tests for normality and homogeneity of variance. Following a significant result, post-hoc multiple comparisons were conducted on mean dates between each habitat treatment (Zar 1996). I conducted post-hoc power analyses using the program GPOWER (Faul and Ehrdfelder 1992).

I compared site fidelity for males and females individually, using logistic regression models (Hosmer and Lemeshow 1989). The binary dependent variable, site fidelity, was coded as 1 = fidelity, 0 = no fidelity. The independent variables I used were date of capture, habitat type, proportional body condition, fat score, reproductive rank, and year. Prior to running the logistic regression models, I performed Pearson bivariate correlations on all variables in each model to reduce the chances of multicollinearity (Menard 1995). Variables that were highly correlated ($p < 0.05$), were selectively

excluded from the model. In these cases, I dropped the variable that was less ecologically relevant, or retained the variable which was correlated with fewer independent variables. For instance, I retained date of capture and dropped body condition, since both were highly correlated. Date of capture was analogous to body condition, as birds captured later in the season were also in better condition. I used the forward conditional method for entry in all models, with 0.10 as the probability for variable entry and 0.15 as the probability for removal from the model. In most instances, a value of 0.05 is considered too low for entry, often excluding important variables from the model (Menard 1995). I present the results for the final model, based on which of the simultaneous models best predicted site fidelity in both male and female White-throated Sparrows. This final model was determined using classification tables, which compare predicted fidelity from observed fidelity, based on the variable included in the model. In attempting to quantify which variable best predicted fidelity, I was most interested in the model which correctly classified the greatest amount of fidelity. I used a classification cut-off of 0.5. In addition to the classification table values, I also report the Nagelkerke R^2 and the model Chi-square for the final model. The Nagelkerke R^2 is comparable to the R^2 obtained in a linear regression, and is defined as the proportion of variance in the dependent variable explained by the regression model (Nagelkerke 1991). The model Chi-square tests the null hypothesis that, except for the constant, the coefficients for all of the variable in the final model are equal to 0, comparable to the overall F statistic in a regression (SPSS Inc. 1994). Given the relatively low sample sizes, I considered $\alpha = 0.90$; $p \leq 0.10$ to be significant.

I used stepwise multiple regression to test the effect of habitat quality indices on dispersal distances in White-throated Sparrows exhibiting breeding site fidelity. Again, I performed Pearson bivariate correlations on all variables prior to running the regression models, and dropped variables that were ecologically similar to other independent variables and were highly correlated ($p \leq 0.05$). I used a probability of 0.10 for entry into the model and a probability of 0.15 for removal from the model. I present results for the final model which best explained the dispersal distances between successive years of male and female White-throated Sparrows.

I used a Kolmogorov-Smirnov goodness of fit test with Lillefors correction to examine the normality of both my dependent and independent variables in all analyses, and tested for homogeneity of variance using Levene's test (SPSS 1999). Unless otherwise stated, I used an alpha level of 0.10. All values represent means ± S.E. All analyses were performed using SPSS (version 10.0) (SPSS 1999).

4.3 - Results

4.3.1 - *Breeding chronology*

In 1999, differences in mean arrival date of male White-throated Sparrows on territories, between habitats, was marginally significant (one-way ANOVA; $F = 2.67$, $df = 2$, $p = 0.07$). Birds arrived on edges marginally earlier than in clearcuts ($p = 0.09$), however, there were no differences between edges and interior forest ($p = 0.99$), or between clearcuts and interior forest ($p = 0.19$). In 1999, the mean date of occupancy in both edge and interior forest habitat was 13 May, with a mean date of occupancy of 16 May in clearcuts (Figure 4.1). In 2000, the mean date of territory occupancy was 14 May in edge habitat, 10 May in clearcuts, and 13 May in interior forest (Figure 4.2);

differences, however, were not significant (one-way ANOVA; F = 0.97, *df* = 2, *P* = 0.39) Power to detect this difference was low, at 0.21.

The first date that males were observed with mates, or were paired, was somewhat more variable between habitats than the arrival of birds on territories. In 1998, the mean date of first pairing was 4 June in edge habitat, 28 May in clearcuts, and 25 May in interior forest habitat (Figure 4.3). However, mean first date of pairing was not significantly different between habitat types (Kruskal-Wallis ANOVA; $\chi^2 = 3.42$, $df = 2$, $p = 0.18$). Power to detect this difference was 44%. In 1999, the mean date of pairing was 23 May in both edge and interior forest and was 18 May in clearcuts (Figure 4.4), and this difference was significant (Kruskal-Wallis ANOVA; $\chi^2 = 13.02$, $df = 2$, $p = 0.001$). In post-hoc Tukey-type multiple comparisons, there was no significant difference in pairing dates between edge and interior forest habitat ($Q = 0.74$, $Q_{0.05, 3} = 2.394$, $p > 0.10$) or between clearcut and interior forest habitat ($Q = 2.20$, $Q_{0.05, 3} = 2.394$, $p > 0.10$), however there was a significant difference between edge habitat and clearcuts ($Q = 2.47$, $Q_{0.05, 3} = 2.394$, $p < 0.10$). The mean date of fledging was not significantly different between habitats in 1998 ($F = 1.14$, $p = 0.33$)(Figure 4.5), or in 1999 ($F = 0.47$, $p = 0.63$)(Figure 4.6). Power to detect these differences was low, at 0.24 in 1998, and 0.12 in 1999.

4.3.2 - *Site fidelity*

A total of 39.7% (29/73) of male White-throated Sparrows returned to the same plot occupied in the previous breeding season (Figure 4.7). Site fidelity was 43.8% (14/32) in edge habitat, 23.1% (3/13) in clearcuts, and 42.9% (12/28). Fidelity in male White-throated Sparrows was positively associated with the date of capture of individual

birds (model $\chi^2 = 3.77$, $p = 0.06$, $R_N^2 = 0.07$). The model correctly classified 24.1% of males returning to plots in the following breeding season and 84.1% of males not returning. Although date of capture itself may be ecologically unimportant from the perspective of a bird deciding whether to return to a breeding site, it was highly correlated with proportional body condition ($p = 0.01$). The mean date of initial capture of banded birds which returned to the same plot the following year was 7 June, whereas for those that did not return it was 30 May.

A total of 6 (16.2%) female White-throated Sparrows returned to the same plot in the following breeding season (Figure 4.8). Site fidelity was 27.3% (6/22) in edge habitat, 0% (0/3) in clearcuts, and 0% (0/12) in interior forest. Fidelity in female White-throated Sparrows was positively associated with both habitat type and breeding rank from the previous year (model $\chi^2 = 12.44$, $p \leq 0.002$, $R_N^2 = 0.46$). These two variables correctly classified 71.4% of returning females and 80.0% of females which did not return. The mean breeding rank of those female which did return was 4.43 ± 0.43, and was 2.70 ± 0.30 for those that did not return.

4.3.3 - *Dispersal distance*

For male White-throated Sparrows, mean breeding rank from the previous breeding season best predicted the dispersal distances of individuals returning to plots in the following breeding season ($p = 0.05$, $R^2 = 0.08$). Males which achieved a rank of one (unpaired) in the previous breeding season, dispersed an average of 180.67 ± 86.31 m, whereas males which achieved a rank of 5 (fledging success), dispersed an average of 35.61 ± 7.03 m. For females, no variables predicted the dispersal distances of individuals returning to plots in the following breeding season ($p = 0.51$). This model was

compromised by the small sample size of females returning to plots in the following season ($n = 6$).

4.4 - Discussion

I made three predictions with respect to habitat quality for the White-throated Sparrow: 1) that individuals in highest quality interior forest habitat would arrive, pair, and fledge young before individuals in other, lower quality habitats; 2) that site fidelity would be greater in interior forest habitat; and 3) that dispersal distance would be lowest in interior forest habitat. For males, my results were not consistent with any of my predictions. The breeding chronology of males in interior forest habitat was not significantly different from males in other, lower quality habitats. In 1999, males in lowest quality clearcuts were paired significantly earlier than males in higher quality, edge habitat. Males showed no consistent patterns with respect to site fidelity or dispersal. For females, my results were again not consistent with respect to any of my predictions, however, sample sizes were very low for all analyses. Males did, however, exhibit significantly higher rates of site fidelity than females, a result consistent with other studies.

4.4.1 - *Breeding chronology*

Male White-throated Sparrows settled habitats of different quality in a random pattern. The majority of male White-throated Sparrows arrive on the breeding grounds during a very narrow window in early May (K. H. unpubl. data). Contrary to other studies (Brown 1969, Alatalo et al. 1984, Lanyon and Thompson 1986, Arcese 1987, Bensch and Hasselquist 1991, Aebischer et al. 1996), male White-throated Sparrows were not settling habitats in response to their quality, in particular, in response to

potential reproductive success or pairing success. Inexperienced birds arriving early on the breeding grounds may later be evicted by more dominant individuals or those birds returning to breeding sites from the previous year (Nolan 1978, Lanyon and Thompson 1986, Jakobsson 1988), thereby uncoupling the hypothesised relationship between settlement rate and habitat quality. Although I did not statistically compare the arrival dates of novice and resident males, residents arrived marginally later, on average, in both years. Resident birds may not need to arrive earlier on the breeding grounds to ensure that they will acquire their territory from the previous year, or an equally suitable territory, if they can evict inexperienced or novice birds which have settled territories prior to their arrival. In my study, several birds banded early in the breeding season later dispersed and were replaced by other breeding individuals.

The mean date of pairing was also variable between years, with no one habitat type having consistently early pairing success. In 1999, pairs formed earlier in clearcuts than in edge plots, but not earlier than interior forest plots. However, clearcuts consistently had lower sample sizes than edge habitat. In addition, pairing of males in clearcuts was concentrated towards the earlier part of the breeding season. In 1999, the last date a pairing was recorded in clearcuts was 30 May, whereas in edge and interior forest, pairs continued to form up until 23 June. Possibly, a small number of high quality males are paired in clearcuts early in the breeding season. In edge and interior forest habitats, late arriving females continued to pair with males in these habitats, rather than pairing with low quality males remaining in, or recently settling, territories in clearcuts. Evidence for this also comes from a small number of polygynous matings in edge habitat and one case of polygyny in interior forest. These results are unusual, given that this

species is assumed to mate monogamously (Falls and Kopachena 1994). The 'polygyny threshold' hypothesis suggests that the fitness of a female who mates polygynously in high quality habitat may be equal to or better than the fitness achieved by mating monogamously in low quality habitat (Wittenberger 1980, Quinney 1983, Petit 1991). Females may recognise that clearcut habitat is inferior to forested habitats within this landscape, and may be providing a more 'honest' indication of habitat quality than males (Wander 1985, Gibbs and Faaborg 1990, Villard et al. 1993, Hunt 1996). Evidence of this can also be seen in the lower pairing success of males in clearcuts (42%), as compared to edges (65%) and interior forests (78%).

Although there were some chronological differences in the patterns of pairing, there were no significant differences in the mean date that young were first observed on territories. It is possible that either weather conditions or food availability may be limiting pairs attempting to produce either early or late broods. These conditions may be optimised during a narrow period of time during the breeding season, as weather may restrict temporal variability in breeding, resulting in a brief and concentrated fledgling period. No territories successfully produced a second brood in this study.

4.4.2 - *Site fidelity*

The proportion of male White-throated Sparrows returning to breeding sites in this study was slightly below average values (39.7% vs. 47%) from studies conducted in Algonquin Park, Ontario (Lowther and Falls 1968, Knapton et al. 1984). For females, site fidelity in this study was higher than average values from these studies (16.2 % vs. 8%). Differences in regional site fidelity in White-throated Sparrows may reflect the comparative isolation of populations (Falls and Kopachena 1994). For example, in

Adirondack Park, New York, rates of site fidelity were much higher for both male and female White-throated Sparrows, probably a result of the parks relative isolation (Tuttle 1993). If site fidelity is influenced by the amount of suitable breeding habitat at the landscape scale, this may explain differences between rates of male fidelity in my study and average values from Algonquin Park. No large-scale deciduous logging has ever occurred in the region surrounding my study (Strong 1992). Fragmentation of the landscape in this area is quite low and suitable habitat for White-throated Sparrows is abundant. Sites used by Knapton et al. (1984), were in the highly developed, southern portion of Algonquin Park, where suitable high quality habitat in the surrounding landscape may have been limited and patchily distributed, resulting in higher overall rates of site fidelity. However, this does not explain the high rates of site fidelity for females in my study. Females exhibit higher rates of site fidelity and reduced dispersal as they age (Ens et al. 1993, Dhondt and Andriaensen 1994, Part 1995). It is possible that the females which did return to breeding sites in my study were also older birds. However, because I was unable to determine the age of birds, and given the limited temporal scale of my study, I cannot quantify the role of age in patterns of female site fidelity.

For males, the date of capture best explained the fidelity of birds to breeding sites. However, this model correctly classified only 24% of those birds which did return and explained only 7% of the variation in male White-throated Sparrow site fidelity. Surprisingly, neither habitat quality (Baeyens 1981, Newton and Marquiss 1982), nor previous nesting success (Dow and Fredga 1983, Gratto et al. 1985, Weatherhead and Boak 1986, Gavin and Bollinger 1988, Haas 1998) were strong predictors of site fidelity. Inter-annual variation in some resource, such as food quantity or quality (Oring 1982),

which I did not measure, may have a greater influence on site fidelity in male White-throated Sparrows than any of the parameters I measured. For females, the mechanisms for site fidelity were more obvious. Both habitat type and female breeding rank in the previous breeding season contributed to site fidelity in female White-throated Sparrows. The regression model correctly classified 71% of returning birds and 80% of those that did not return, and explained 46% of the variation in site fidelity.

Given that females with higher reproductive ranks in the previous year were more likely to return than those with lower ranks, based on previous success, female White-throated Sparrows may be better able to assess habitat quality than males. However, females only returned to edge habitat, which did not have the highest overall mean reproductive rank. Individual success, and not overall success (Bollinger and Gavin 1989, Cadion et al. 1993) appears to account for higher rates of site fidelity in female White-throated Sparrows. Why successful females in interior forest habitat, which had the highest overall reproductive success, did not return is puzzling. In a landscape such as the mixed-wood boreal forest, where natural fire was once the dominant form of disturbance (Bunnell 1995), natural edges formed by fire may have historically represented optimal or source habitat. With the advent of large-scale clear-cutting, anthropogenic edges, may be functionally different than natural edges. Birds may return to edges at higher rates, despite there being vacancies in nearby better quality interior forest habitat as a result of an adaptive preference for edges. However, without knowing if edge habitat in my study area functions as a reproductive 'sink', I cannot assess whether high fidelity in this habitat is negatively impacting White-throated Sparrow populations.

Further investigation of the mechanism(s) for male breeding site fidelity and female dispersal may provide greater insight into the role of habitat quality for White-throated Sparrow populations. However, because there is a strong bias towards recording singing male birds using common census techniques such as point counts, males may not be providing a measure of habitat quality for White-throated Sparrows. In this study, however, female site fidelity and habitat use also seem to be providing a poor measure of habitat quality. Without a greater understanding of the role of habitat quality in most fragmentation studies, management recommendations based on male habitat use alone seems moot. Considering previous work (Chapter 3), the most reliable measures both in accuracy and potential conservation value are pairing success and reproductive success. Without measuring these variables, studies using only the density or abundance of singing males to assess habitat quality may be providing unreliable results.

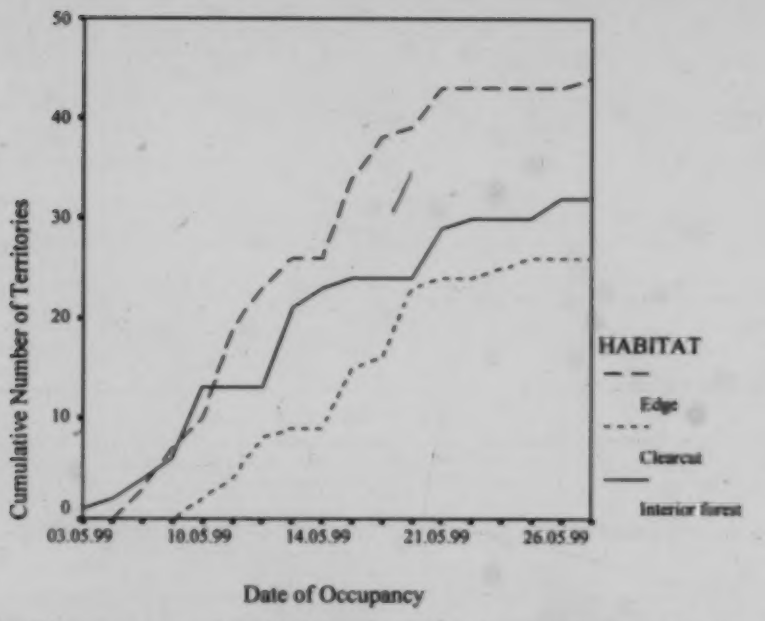

Figure 4.1 – Settlement pattern of territorial male White-throated Sparrows in edge, clearcut, and interior forest habitats in 1999.

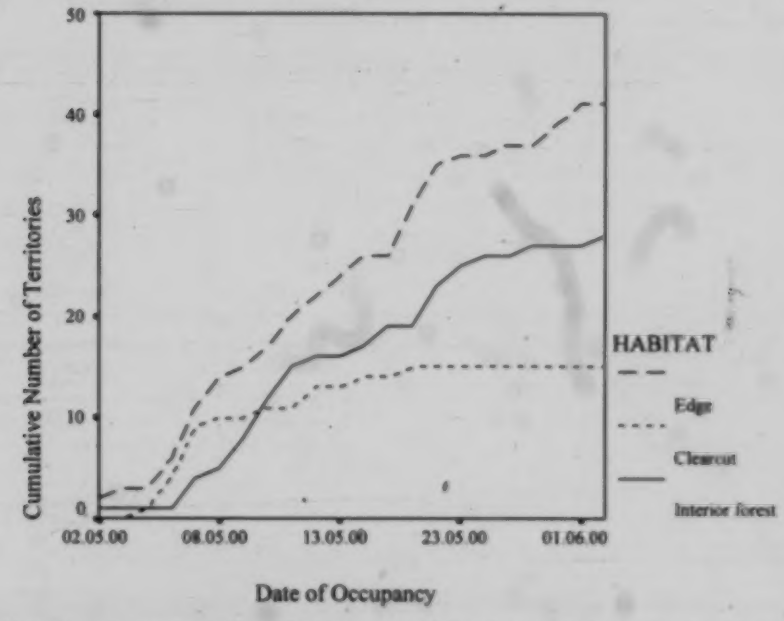

Figure 4.2 – Settlement pattern of territorial male White-throated Sparrows in edge, clearcut, and interior forest habitats in 2000.

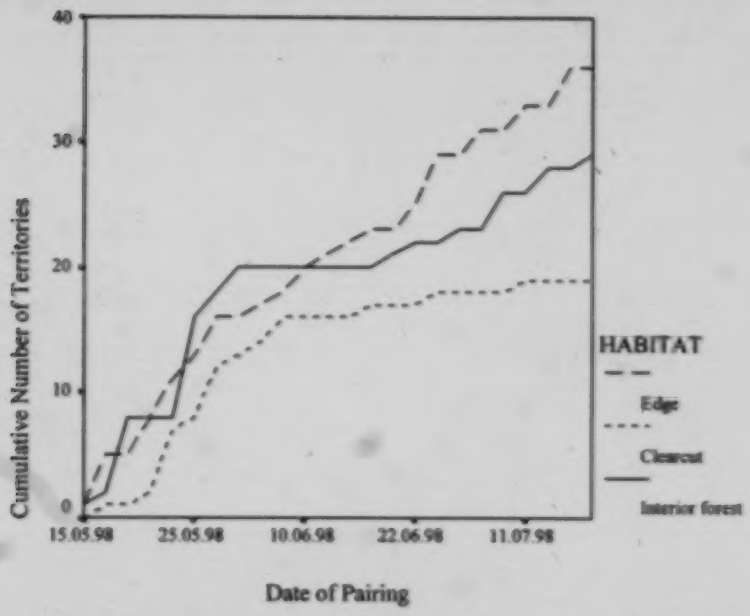

Figure 4.3 – Date of confirmed pairing of territorial male White-throated Sparrows in edge, clearcut, and interior forest habitats in 1998.

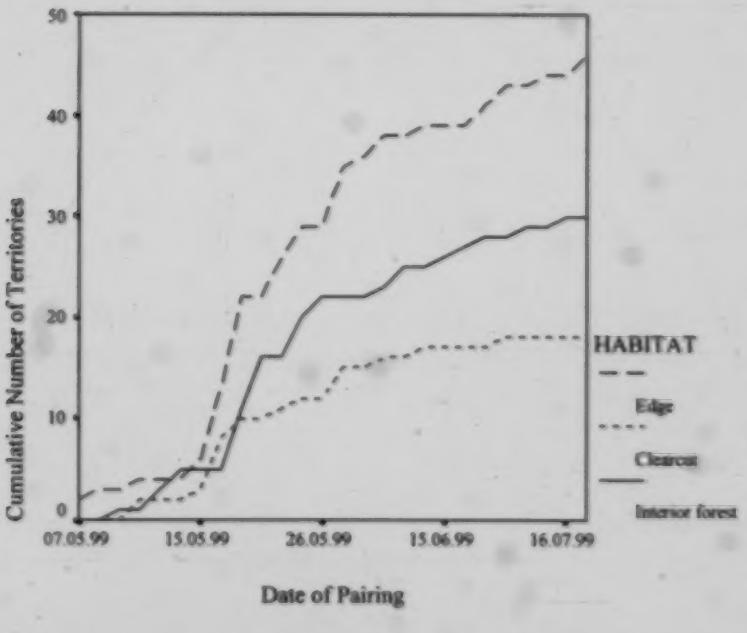

Figure 4.4 – Date of confirmed 'pairing' in male territorial White-throated Sparrows in edge, clearcut, and interior forest habitats in 1999.

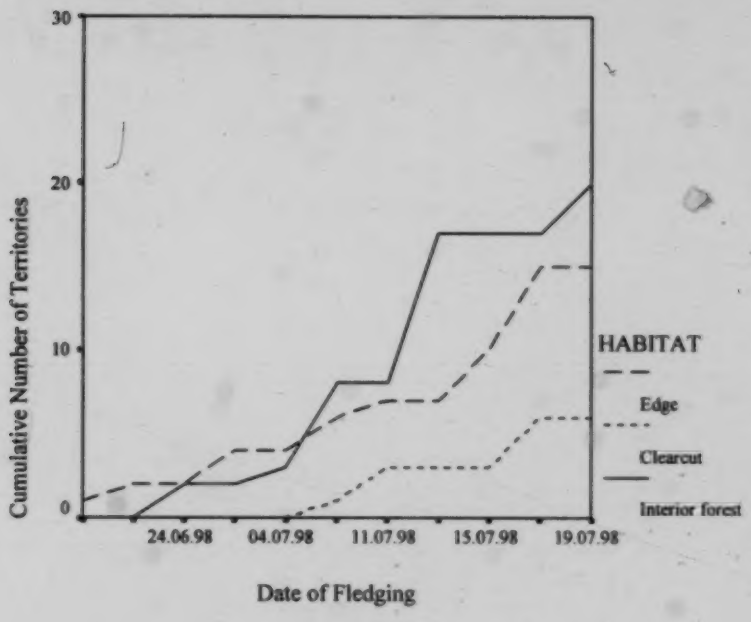

Figure 4.5 – Date of first observation of juvenile White-throated Sparrows for territories in edge, clearcut, and interior forest habitats in 1998.

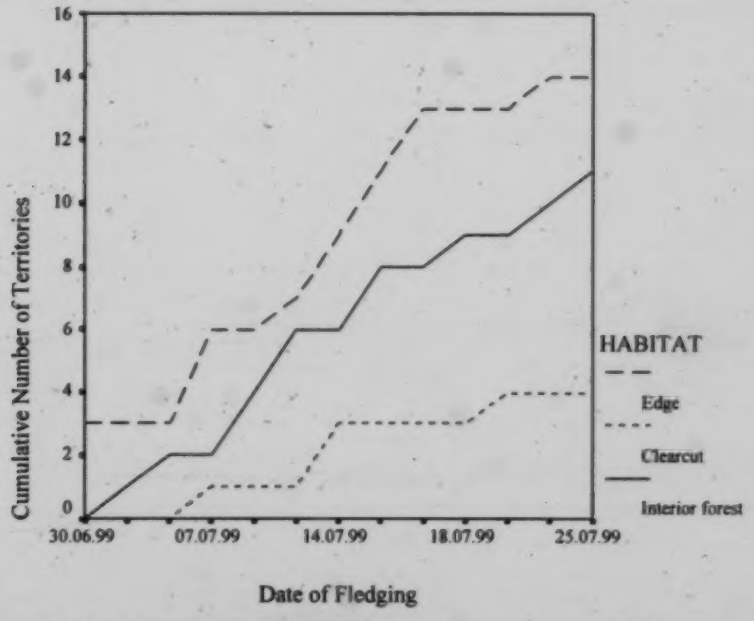

Figure 4.6 – Date of first observation of juvenile White-throated Sparrows for territories in edge, clearcut, and interior forest habitats in 1999.

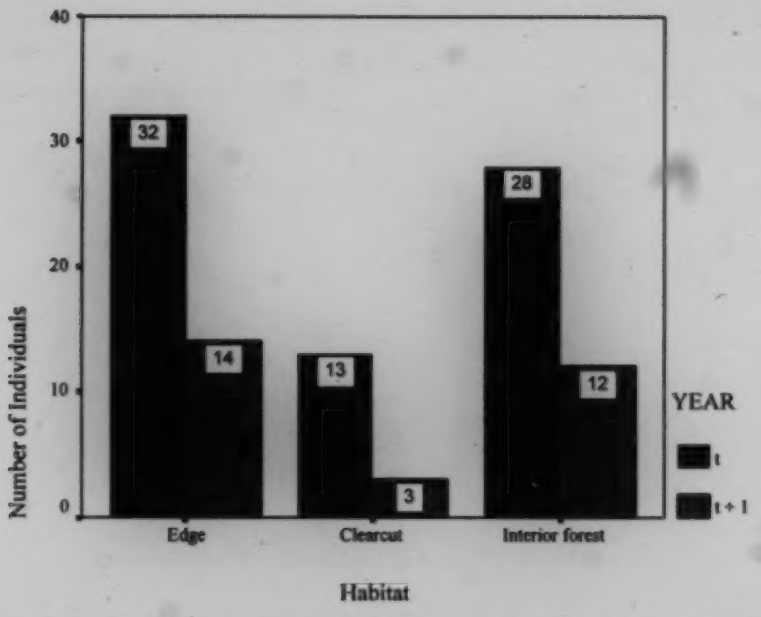

Figure 4.7 – Site-fidelity in male White-throated Sparrows in edge, clearcut, and interior forest habitats. Year t represents the number of banded individuals in a given year; year t + 1 represents the number of individuals returning to that habitat the following year.

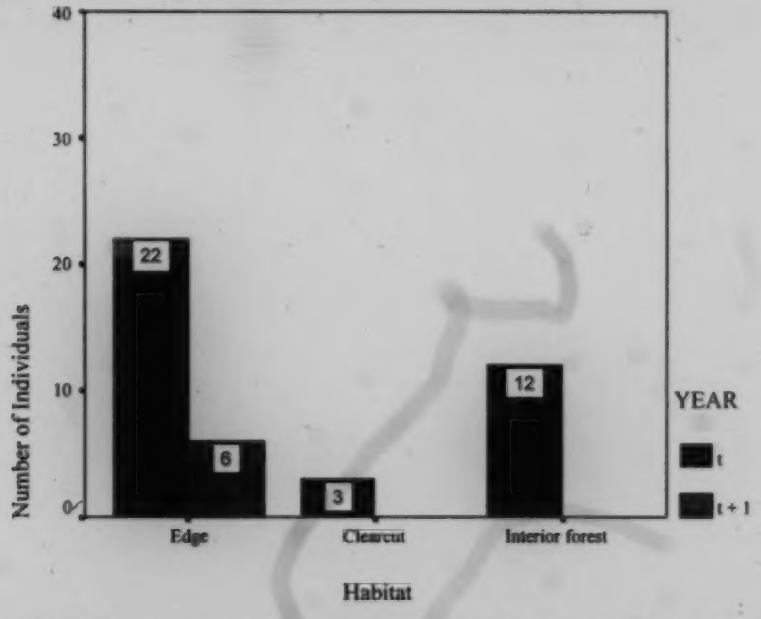

Figure 4.8 – Site fidelity in female White-throated Sparrows in edge, clearcut, and interior forest habitats. Year t represents the number of banded individuals in a given year; year t + 1 represents the number of individuals returning to that habitat the following year.

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CHAPTER 5 – CONCLUSIONS, MANAGEMENT RECOMMENDATIONS, AND FUTURE RESEARCH.

My overall objective in this thesis was to assess White-throated Sparrow population responses to forest harvest. In addition, I evaluated whether density accurately reflected patterns in habitat quality for a population of White-throated Sparrows. Given the strong reliance on density as an indicator of habitat quality, I wanted to assess how reliable this relationship was, specifically in guiding management decisions for this species. In Chapter 2, I compared the territory density of this species with four possible indices of habitat quality. In Chapter 3, I evaluated habitat quality across a range of three habitat types in a recently harvested and patchy landscape, to investigate whether forest harvesting was negatively affecting habitat quality for this species. In Chapter 4, I compared the breeding chronology, site fidelity, and dispersal of this species across the same three habitat types, to further quantify habitat quality.

5.1 – *Density as an indicator of habitat quality*

Territory density provided a poor measure of habitat quality for White-throated Sparrows between habitats of different quality. Of the five indices I used to test relationships between density and habitat quality, none were significantly correlated. For White-throated Sparrows, density should not be used as a sole means of assessing short-term population responses to habitat alteration. A sampling method which does not accurately measure nor provide direct quantitative evidence of decline will not provide suitable information for designing and implementing appropriate management strategies.

Debate continues as to whether declines in migratory songbirds are a result of habitat alteration on the breeding grounds (Böhning-Gaese et al. 1993, Robinson and

Wilcove 1994), during migration (Hutto 2000), or on the wintering grounds (Sherry and Holmes 1996). Without evaluating reproductive success, it may be difficult to directly implicate habitat changes on the breeding grounds. Future research should be aimed at addressing which stage of a bird's annual life-cycle is being negatively impacted, thereby resulting in the declines. More detailed study of short-distant migrants during migration and on wintering grounds in the contiguous United States is necessary.

Of the indices I used to assess habitat quality for White-throated Sparrows, beyond measures of reproductive success, only proportional body condition was an accurate measure. For this species, obtaining data on the body condition of birds through capture in mist-nets may provide an effective means of assessing habitat quality. For other species, banding studies which compare proportional body condition in habitats of different quality are needed to test the effectiveness of this technique. Although used as a standard method of assessing habitat quality, reproductive success can be difficult to measure (see summary in Vickery et al. 1992). For White-throated Sparrows, and potentially, other ground nesting species, the use of a reproductive index to assess reproductive success may be a suitable alternative to locating and monitoring actual nests (Vickery et al. 1992). Comparison of this index with the success of actual nests suggests that it provides a fairly reliable and accurate measure of reproductive success (Vickery et al. 1992, Rangen 2000, Chapter 3, this study). However, despite being a time-efficient means of obtaining data on reproductive success, this method is not appropriate for all species. White-throated Sparrows are large, conspicuous, and highly abundant passerines, making them ideal candidates for such an index method. Before applying this

reproductive index to other species, researchers should consider natural history attributes to assess whether this index is appropriate.

Alternatively, pairing success of male birds has increasingly been used as a surrogate measure of habitat quality for passerine species (e.g. Villard et al. 1993, Hunt 1996). Although relationships between pairing success and reproductive success seem implicit, few studies have made quantitative comparisons of these two indices. My results suggest that, for White-throated Sparrows, pairing success provides a good surrogate measure of reproductive success. In addition, determining rates of pairing success is an efficient means of assessing reproductive success, and potentially, habitat quality. For other species, relationships between pairing success and reproductive success should be quantitatively assessed prior to using this method as a sole means of evaluating reproductive success or habitat quality. In addition, efforts to develop a more time-efficient means of censusing the presence of females in different habitats seems warranted, given they may exhibit greater habitat selectivity than males .

5.2 – *Habitat quality for White-throated Sparrows*

Results from this study suggest that recent clearcuts do not provide good quality habitat for White-throated Sparrows. Clearcuts had significantly lower rates of pairing success and reproductive success than interior forest habitat, and these rates were also marginally lower than in edge habitat. Of the three habitats I compared, interior forest represented the highest quality habitat for this species, as reflected by mean values of habitat quality indices. Although habitat quality was slightly lower in edges, relatively high reproductive success and high site fidelity suggest that edge populations may be self-sustaining. Clearcuts, on the other hand, probably do not support self-sustaining

populations, possibly resulting in asynchronous gene flow from high quality habitat into low quality clearcuts (*sensu* Dias 1996). I speculate that in my study area, clearcuts represent reproductive 'sinks' (sensu Pulliam 1988), however, I was unable to provide quantitative evidence of this assertion.

I only studied habitat quality in 5-6 year old clearcuts, and data which span a much broader temporal range of regenerating forest are necessary to fully evaluate the implications of forest harvesting on this species. Comparisons of habitat quality between clearcuts and burned forest of comparable age, structure, and size are also needed. Comparing habitat quality between these two forest types will help to assess the effectiveness of forest harvesting strategies aimed at emulating wildfire. Density comparisons between post-harvest and post-fire habitats suggest that White-throated Sparrows occur in greater densities in post-fire habitats for up to 28 years (Hobson and Schieck 1999). However, these comparisons are based solely on density and do not provide any measure of habitat quality.

5.3 – *Breeding chronology, site fidelity, and dispersal*

Breeding chronology, site fidelity, and dispersal did not provide good measures of habitat quality for male or female White-throated Sparrows in this study. Individuals established territories and fledged young on similar dates among habitats. In 1999, pairing occurred significantly earlier in clearcuts than in edge or interior forest habitat. However, both mean territory density and overall pairing success were lowest in clearcuts. The few males which did successfully pair with females in clearcuts, did so relatively early. However, males in edge and interior forest habitat continued to establish territories and pair with females throughout the entire breeding season, in contrast to

males in clearcuts. Additionally, some females opted to mate polygynously in higher quality edge and interior forests, rather than mate with males in clearcuts, suggesting this habitat was of poor quality.

Site fidelity in male White-throated Sparrows was significantly higher than in females (see also Falls and Kopachena 1994). Patterns in female site fidelity, however, were much more apparent than in males. Females only returned to edge habitats, whereas males returned to all habitats in equal proportions, irrespective of their quality. For females, but not for males, mean overall reproductive rank from the previous breeding season was a strong predictor of site fidelity. It appears that females are better at assessing habitat on the breeding grounds than are males, a result consistent with other studies (Villard et al. 1993, Hunt 1996). Therefore, survey methods which consist of censusing territorial males (i.e. point counts) may inherently misrepresent habitat quality.

Others have suggested there is a strong relationship between reproductive success and breeding dispersal (Jakobsson 1988, Haas 1998), and male dispersal distance was negatively correlated with overall mean reproductive rank. Males that were successful in one year tended to disperse shorter distances the following year than did unsuccessful males. However, this model only accounted for a small proportion of the total variation and was only marginally significant. For females, small sample size (n = 6) precluded quantitative assessment of the factors influencing dispersal distance. Given the large investment necessary to obtain this type of data, results from this study do not support this measure as an efficient means of quantifying habitat quality.

Studies which have used breeding chronology, site fidelity, and dispersal in assessments of habitat quality for migratory passerines have generally been conducted in

highly fragmented landscapes, where optimal habitat may be less available and more patchily distributed. In contrast, the landscape surrounding my study site was more continuous and relatively intact, and optimal habitat may be more widely distributed, with high connectivity facilitating greater dispersal of birds. If birds do disperse greater distances, the result would be much lower rates of site fidelity. In addition, if optimal habitat is not limited, there may be less advantage to arriving early on the breeding grounds. Birds arriving on the breeding grounds later in the spring, having maintained a higher reserve of fat, may be in better breeding condition upon arrival. Improved body condition may improve reproductive success. At this high latitude, early spring weather may impose a greater cost to the survival of birds that arrive early, outweighing any potential advantage gained in securing a territory. Therefore, the use of these three indices as a means of assessing habitat quality for the White-throated Sparrows, and potentially other migratory passerines, seems limited.

5.4 – *Conservation and management of White-throated Sparrows*

Falls and Kopachena (1994) estimated the entire North American population of White-throated Sparrows at 20 – 40 million individuals, making it one of the most abundant native passerine birds throughout its range. Given its high relative abundance and distinctive song, the White-throated Sparrow is also one of the most commonly recorded songbirds along Canada-wide Breeding Bird Survey (BBS) routes (Downes et al. 1999). Between 1966 and 1996, (BBS) trend data suggest that significant annual population declines of 1.1% have occurred. Although no management is currently warranted for this species, reasons for the range-wide declines of this species remain puzzling. Declines may reflect rates of permanent habitat loss or land conversion to non-

forested uses across this species range, however further study is necessary to substantiate this hypothesis.

This study represents the first quantitative assessment of reproductive success and habitat quality across a range of habitat types for the White-throated Sparrow. Overall, rates of reproductive success in this study (34.8%) were considerably lower than rates in the published literature (Falls and Kopachena 1994). These results may provide the first line of evidence implicating habitat changes on the breeding grounds as a potential causal mechanism for observed declines in this species, however, continued monitoring is necessary. To fully quantify the effect of habitat changes occurring on the breeding grounds, information on reproductive success is needed from across this species' range. In particular, estimates of reproductive success across habitat types should be made in northern Ontario and northern Quebec, where this species reaches its highest densities (Falls and Kopachena 1994).

Although habitat assessments conducted using density may be efficient, the resulting data may not accurately reflect actual patterns of habitat quality. However, it may not be possible to evaluate habitat quality for every species using detailed evaluations. Certain species may act as suitable 'indicators' of habitat quality for other species with ecologically similar resource requirements, however their effectiveness remains unclear (Taper et al. 1995, Niemi et al. 1997, Jansson 1998). Irrespective, sampling techniques which efficiently incorporate some measure of habitat quality are required. Until then, results from short-term studies which do not directly measure habitat quality may be of limited value, particularly for habitat generalists, and results should be carefully evaluated prior to deciding on management actions.

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